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TITLE: The Possible Participation of Growth Stimulants and Nucleic Acids in the Mechanism of the Action of Phytochrome

/O bozmozhnom uchastii rostovykh veshchestv i nukleinovykh kislot v mekhanizme deystviya fitokhroma/

AUTHOR: M. B. Shternberg , All-Union Institute for Scientific and Technical Information of the Academy of Sciences, USSR

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information which is available in published literature on the role of phytochrome.

Basic research in the field of photomorphogenesis has been conducted during the course of the last 20 years by a group of American scientists headed by Borthwick and Hendricks (Beltsville, Maryland, USA). The successes which have been achieved by these researchers are explained mainly by the fact that the group combines representatives of various related specialties -- chemists, physicists, plant physiologists, and botanists. This integrated conduct of research has made it possible for the first time to give a quantitative evaluation of the effect of light of various wave lengths on the morphogenesis of plants. Now many plant physiologists have become interested in studying the photomorphogenesis of plants and a large number of works has accumulated on this subject; a whole book would not be sufficient for a full description of all these works.

The basic purpose of this present survey is to attempt to analyze the contradictory experimental data which are available with respect to the mechanism of the physiological action of light through phytochrome. However, inasmuch as up to the present time there are no summaries which have been published in Russian on this theme, we have felt it to be necessary to give a brief description of the history of the question and to describe the current trends in the investigation of phytochrome*.

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* In foreign literature there are good surveys with respect to phytochrome in works by Mohr (1960, 1962, 1964), Borthwick and Hendricks (1961), and also Rolin (1964a).

The History of the Study of Phytochrome

The contribution of the Beltsville scientists has not been that they discovered the effect of the spectral composition of light on the morphogenesis of plants. Phenomena of this kind were already known previously with respect to photoperiodism, the germination of seeds, and the growth of seedlings (Katunskiy, 1937; Flint, McAlister, 1937; Went, 1941; Kleshnin, 1946). The Beltsville researchers succeeded with the help of a specially designed highly sensitive spectrograph in making a quantitative study of the action spectrum of visible light with respect to various aspects of morphogenesis. They determined the light energy of various wave lengths necessary in order to obtain an effect in 50% of the cases. The first objects which were studied in this way were short-day plants -- soybean and cocklebur, the floral initiation of which is prevented upon the interruption of the photoinductive dark period by several minutes of illumination. Parker, Hendricks, Borthwick, and Scully (1945, 1946) established that red beams with a wave length of 600-680 millimicrons are most effective in this case (for the suppression of

floral initiation in 50% of the cases it is sufficient to have energy of 3-5•10^4 ergs/cm^2). The similarity of the data which were obtained with the absorption spectrum of chlorophyll led the authors to the idea of using the red light absorbed by the chlorophyll in order to disrupt the flowering stimulus.

In subsequent works by Beltsville researchers (Borthwick, Hendricks, and Parker, 1948; Parker, Hendricks, and Borthwick, 1950; Parker, Hendricks, Borthwick, and Went, 1949) a similar action spectrum was obtained with respect to the stimulation of the floral initiation of long-day plants (barley, henbane) and also with respect to intensification of the growth of the leaves and weakening of the growth of internode sections of etiolated pea seedlings. Already during the course of these investigations a hypothesis was expressed with respect to the presence of a particular pigment connected with the morphogenetic action of light on plants.

This hypothesis has found experimental support as a result of the study of the spectrum of action of light on the germination of lettuce seeds (Borthwick, Hendricks, Parker, Toole, Toole, 1952).

The thing which was new in principle in this work was the establishment of the antagonistic action of red light and far-red light; red light (maximum of 630-660 millimicrons) stimulated the germination of light-germinating seeds; far-red light (maximum of 720-740 millimicrons) removed the effect of red light. In the case of repeated alternation of red light and far-red light the reaction of the plants depended on the subsequent irradiation.

On the basis of these data a bold hypothesis was advanced which has turned out to be extremely fruitful upon experimental verification; red light and far-red light are absorbed by two forms of one and the same pigment. In darkness the plants contain the form with a maximum of absorption at 650 millimicrons; upon the absorption of red light this form is converted into the other form with a maximum of absorption at 730 millimicrons. This second form, in turn, upon the absorption of far-red light or in the case of darkness is converted into the first one.

The hypothesized mutual transformations of the forms of the pigment have been expressed by the following scheme, all elements of which are unknown:

	Red Light	
Pigment + RX	⇄	Pigment X + R
(maximum 650 millimicrons)	Far-red light	(maximum 730 millimicrons)
At rest	Darkness	Germination

Substrate + RX ⇄ R + Substrate X

Subsequently there was a description of the photoreversibility of other morphogenetic reactions of plants based apparently on the presence of the same two forms of the hypothetical pigment. Thus, in the case of the short-day plants cocklebur, soybean, amaranth, and chrysanthemum the interruption of the photoinductive dark period by brief illumination with red light prevented floral initiation; irradiation with far-red light removed the effect of red light (Borthwick, Hendricks, Parker, 1952; Downs, 1956; Cathey, Borthwick, 1957). In the case of long-day plants -- barley and henbane -- red light, on the other hand, caused floral initiation if it acted during the middle of the dark nonphotoinductive period. And in this case far-red light had an antagonistic effect (Downs, 1956). The data which were obtained led the authors to the idea that biological activity is possessed by the form of the pigment with a maximum of absorption in the region of 730 millimicrons (P_{730}), whereas the form with a maximum of absorption in the region of 660 millimicrons (P_{660}) is inactive:

$$P_{660} \underset{\text{Far-red light, Darkness}}{\overset{\text{Red light}}{\rightleftarrows}} P_{730}$$

Downs (1955) was able to show the diversity of the reactions which depend on the hypothetical pigment in the case of one and the same object -- etiolated bean seedlings. Red light caused suppression of the growth of the hypocotyl, stimulation of the growth of the epicotyl, opening and growth of the leaves, and straightening of the bending of the apical part of the hypocotyl. Far-red light removed the effect of red light. In the case of green bean seedlings and also of the sunflower and morning glory the growth of the internode sections and the petioles was intensified as a result of brief illumination (after an 8-hour day) with far-red light, the action of which was eliminated by red light (Downs, Hendricks, Borthwick, 1957). These differences in the reaction of etiolated and green seedlings were accounted for by the authors on the basis of the predominance in the plants in the first case of the P_{660} form and the predominance in the second case of the P_{730} form (see also Downs, 1959).

As the tests which were conducted by Downs and Borthwick (1956) demonstrated, the intensification of growth and the delay of the transition of the trees to a state of rest which are observed in the case of an increase in the length of the day also were based on the action of far-red light. Thus, in the case of Catalpa bignonioides raised during an 8-hour day, an additional 8 hours of illumination with far-red light causes stimulation of growth, whereas illumination with red light causes a decrease in the period of growth and a transition to a state of rest. In accordance with these observations while raising plants exclusively with far-red light (incandescent lamps) and red light

(fluorescent lamps), Downs and Piringer (1958a, 1958b) discovered the stimulating effect of far-red light on the growth of trees and also on the growth of cereals. The stimulating effect of far-red light on the growth of trees can have great ecological importance for seedlings, inasmuch as under the canopy of a tree there is a predominance of "infrared shadow" (Shakhov, Khazanov, Stanko, 1965). In the case of cereals far-red light caused acceleration of floral initiation. The effect of far-red light on floral initiation in cereals is being studied at the present time by Friend (1964, 1965).

An antagonistic action on the part of red light and far-red light was also discovered with respect to the biosynthesis of pigments. In the skin of the tomato red light caused the formation of yellow pigment (Piringer, Heinze, 1954). In the seedlings of turnips, red cabbage, mustard, and beans upon irradiation with red light there is a synthesization of anthocyanins (Siegelman, Hendricks, 1957, 1958a; Mohr, 1957; Klein, Withrow, Elstad, Price, 1957). The brief irradiation of etiolated seedlings or separate leaves of wheat and bean with red light caused stimulation of the synthesis of chlorophyll upon their further cultivation under conditions of solar illumination (Virgin, 1957, 1958; Klein, Withrow, Elstad, Price, 1957).

Finally, in 1959 the hypothesis with respect to the presence in plants of a pigment with reversibility of action in the case of red light and far-red light received brilliant confirmation in the investigation of Butler, Norris, Siegelman, and Hendricks (1959); with the help of a highly sensitive differential spectrometer they determined the content of pigment in etiolated seedlings of corn and turnip and separated it from the plants in the form of a partially purified extract. The active basis of the extract which was soluble protein was preserved in vitro with the ability for a reverse shift of the maximum of absorption, the position of which was the same as in the case of in vivo. The authors expressed a concept with respect to the enzymatic activity of the pigment which up to the present time has not received experimental confirmation.

According to the latest data the absorption spectrum of this pigment called phytochrome is similar to the absorption spectrum of allophycocyanin. In connection with this it is suggested that the prosthetic group of phytochrome is bilidiene or bilitriene (Hendricks, 1964). Purification sixty times of the extract obtained from etiolated seedlings of oats made it possible to establish that the molecular weight of phytochrome is 90,000-150,000 (Siegelman, Firer, 1964).

The study of the distribution of phytochrome in etiolated seedlings showed that in monocotyledons (barley, oats, corn) its content is at a maximum in the upper parts of the coleoptile and leaves and in the nodes while in dicotyledons (beans, peas,) its content is at a maximum in the upper part of the epicotyl and at the end of the root (Briggs, Siegelman, 1963; Furuia, Hillman, 1964). With age the content of

phytochrome is reduced. The conversion of phytochrome in darkness from the active form P_{730} to the inactive form P_{660} depends on the temperature and is retarded considerably when the temperature is reduced.

The detection of phytochrome in green plants is made difficult by the presence of chlorophyll with close to the maximum value of absorption in the red region of the spectrum. However, methodological difficulties have been overcome and the presence of phytochrome has been established photometrically in extracts from leaves of green plants of 16 species (Lane, Siegelman, Butler, Firer, 1963). In long-day plants it is considerably easier to detect phytochrome than in short-day plants (negative results which were apparently based on the high content of chlorophyll in the extracts were obtained with chrysanthemum, perilla, soybean, and cocklebur). The content of phytochrome in green plants was considerably less than in etiolated plants. Even such a deliberately simplified and schematic description of the history of the study of phytochrome shows how complex the problem is and how broad the possibilities are for further research in this field.

Current Trends in the Investigation of Phytochrome

It is possible to note three basic current trends in the experimental study of phytochrome.

The spectrum action. This refers to the work which is being done in connection with the identification and precise determination of the spectrum of action of light with respect to various light-sensitive reactions of plants.

In studying the effect of light on the synthesis of anthocyanin in seedlings of Brassica rapa Siegelman and Hendricks (1957) established the presence of two pigment systems -- a low energy system which corresponds to phytochrome and a high energy system with maximums of absorption in the blue (454 millimicrons) and far-red (710 millimicrons) ranges. The activity of the second system upon the use of longer exposures (on the order of several hours) or of higher energy of radiation (greater than 16^{6} erg/cm^{2}).

The study of the high-energy pigment system was continued by Mohr (Mohr, 1957, 1958, 1959a, 1959b; Mohr, Pinning, 1962) firsts at Beltsville and then at Freiburg University (FRG). According to the data by Mohr, in seedlings of Sinapis alba both pigment systems act synergetically, causing the formation of anthocyanin and the appearance of hairs on the hypocotyl and stimulating new formation and the growth of the rudiments of leaves; the suppression of the growth of the hypocotyl is based only on the activity of the high-energy system. Mohr also detected (Mohr, Nes van, 1963; Harraschain, Mohr, 1963) the synergetic action of the two pigment systems in Fagopyrum esculentum in respect to the stimulation of the biosynthesis of anthocyanins and flavonols and the suppression of the growth of the hypocotyl. In contrast

to these objects, in the case of Lactuca sativa the pigment systems act antagonistically -- phytochrome causes bending of the apical part of the hypocotyl and germination of the seeds; the high-energy system removes this effect (Mohr, Noble, 1960; Mohr, Haug, 1962; Mohr, Appuhn, 1963; Rollin, 1963).

Subsequently, Hendricks and other Beltsville researchers rejected the concept of the presence of a particular high-energy system different from phytochrome. They found that in the case of high-energy radiation light of a wave length of 670-720 millimicrons is absorbed by both forms of phytochrome, and they came to the conclusion that under such conditions both forms of the pigment are in an active excited state (Hendricks, Borthwick, 1959a, 1959b; Hendricks, Toole, Toole, Borthwick, 1959). The data which were obtained earlier concerning a spectrum of action of light with respect to the synthesis of anthocyanin in the skin of an apple and of red cabbage and turnip seedlings which was different from phytochrome (Siegelman, Hendricks, 1957, 1958a) could be explained from the point of view of the predominance of the given form of phytochrome in the active state. Hendricks also explained other cases when prolonged irradiation with far-red light has an effect which is similar to the case of brief irradiation with red light by the active condition of both forms of phytochrome (Withrow, Klein, Price, Elstad, 1953; Klein, Withrow, Elstad, Price, 1957; Kasperbauer, Borthwick, Hendricks, 1963).

However, in recent works of the Beltsville researchers factual proof is again being cited with respect to the existence of other pigments in addition to phytochrome. Thus, the synthesis of anthocyanins in seedlings of sorghum is regulated by two photoreactions -- a high-energy photoreaction with a maximum in the region of 470 millimicrons and a long-energy photoreaction with a spectrum of action which is characteristic for phytochrome (Downs, 1961; Downs, Siegelman, 1963). On the basis of experimental data which have been obtained with the use of a specific inhibitor of the transfer of electrons in the case of photosynthesis, the idea is expressed of the similarity of the high-energy system with the first pigment system of photosynthesis which has a maximum of absorption in the region of 680-730 millimicrons (Downs, 1964).

Thus, the question of the presence of a high-energy pigment system in addition to phytochrome and of the interaction of these two systems remains open and requires further investigation.

During the course of the study of the spectrum of the action of light on morphogenesis new reactions appeared as did new objects experiencing the effect of light through phytochrome. There has been a description of the stimulating effect of red light on the geotropic bending of the coleoptile of oats (Blaauw, 1961, 1963) and of mustard seedlings (Mohr, Pichler, 1960) and also a description of the inhibiting action of red light with respect to the geotropism of the coleoptile of

corn (Wilkins, Goldsmith, 1964).

Phototropic bending is caused by uni-directional irradiation with blue light; however, in the case of coleoptiles of oats it is intensified by red light (Blaauw, Jansen, 1959; Briggs, 1963).

The growth of axillary buds of the cocklebur is caused by red light; far-red light removes this effect (Bogorad, McIlrath, 1960).

In the duckweed it was found that there was an antagonistic effect on the part of red light and far-red light not only with respect to blossoming but also with respect to the growth of "runners" (changed leaves) and roots and also with respect to the speed of vegetative multiplication (Kandeler, 1962, 1963).

The growth of the stem in certain long-day plants was also a photoreversible process; in the case of Melilotus alba it is stimulated by red light (Kasperbauer, Borthwick, 1964).

The transformation of phytochrome in plants. In this connection there are works which are devoted to an examination of the condition of the pigment in plants under various conditions of illumination. More than once Hendricks and Borthwick expressed the idea that the speed of the transformation of phytochrome in darkness from the active form to the inactive form is determined by the ability of the plants to "measure" time, i.e., their photoperiodic reaction (Borthwick, Hendricks, 1960; Hendricks, 1963; Hendricks, Borthwick, 1963; Hendricks, 1964; Borthwick, 1964). Numerous tests with short-day plants have shown that their reaction to red light illumination and the reversibility of this reaction in the case of far-red light illumination depend strictly on the period of the light-darkness daily cycle of the processing, the duration of the processing, the length of the night period, and other conditions of the light regime (Takimoto, Ikeda, 1959; Nakayama, Borthwick, Hendricks, 1960; Borthwick, Cathey, 1962; Takimoto, Naito, 1962; Borthwick, Downs, 1964; Fredericq, 1964). In the opinion of the Beltsville researchers, all of these occurrences are based on the peculiar aspects of the state of the phytochrome in connection with the varying speed of its transformation from the one form to the other.

The advocates of the ideas of Bunning with respect to biological clocks deny the decisive importance of phytochrome in the mechanism by which the plant measures time, considering that the sensitivity of plants to the action of light is determined by the endogenous rhythm, while phytochrome influences the photoperiodic reaction of plants only within the limits of this rhythm (Könitz, 1958; Carpenter, Hamner, 1963; Takimoto, Hamner, 1964; Hamner, Takimoto, 1964). At the same time phytochrome can have some influence on the endogenous rhythm, in particular on the rhythm of the movements of bean leaves (Lörcher, 1958). It is completely obvious that the resolution of the contradictions which

have occurred will be possible only after obtaining sufficiently precise information with respect to the transformations of phytochrome in green plants. The study of this question is still only beginning (Butler, Lane, Siegelman, 1963; De Lint, Spruit, 1963; Hillman, 1964; Butler, 1964; Butler, Lane, 1965). However, already the first works showed that the causes of the different sensitivity of a given object to the action of red light and far-red light can be most varied and are not necessarily connected with the properties of phytochrome itself.

Lane (1963) established that three varieties of sorghum with a different photoperiodic reaction under the conditions of a 14-hour day possess different sensitivity to far-red light during the course of the dark period, despite the same speed of the transformation in darkness of phytochrome from the P_{730} form to the P_{600} form.

The reasons for the lesser sensitivity to red light as displayed by the chrysanthemum in comparison with the cocklebur and the soybean turned out to be purely anatomical -- the chlorophyll-bearing cells in the leaf are so densely packed that they capture a considerable part of the red beams (Cathey, Borthwick, 1964).

In the case of etiolated pea seedlings the intensity of the reaction of the leaves, stems, and roots to the action of red light and far-red light is not always in accordance with the content of phytochrome in these organs (Furuya, Torrey, 1964; Furuya, Hillman, 1964).

The mechanism of the action of phytochrome. As was shown above, the most varied reactions of morphogenesis are sensitive to the action of light which has been absorbed by phytochrome; this ranges from germination to blossoming and includes the division, stretching, and differentiation of cells. The sensitivity to light is extremely varied in the individual species and varieties of plants. These differences can be so great as to establish the opposite sign for the action of light of one and the same wave length. Thus, red light retards the floral initiation of short-day plants, but stimulates the floral initiation of long-day plants, intensifies the geotropic bending in the coleoptiles of oats and mustard and weakens it in corn, and causes the straightening of the bending of the apical part of the hypocotyl in bean seedlings and Cuscuta indecora (Downs, 1955; Klein, Withrow, Elstad, 1956; Withrow, Klein, Elstad, 1957; Lane, Kasperbauer, 1965), but stimulates its formation in lettuce, Phacelia tanacetifolia, and Picea abies (Mohr, Haug, 1962; Scharff, 1962; Rollin, 1964c). Lettuce of the Grand Rapids variety is the classical object for the study of the photoreversibility of the germination of seeds, whereas in seeds of another variety such as Great Lakes, this property is manifested only after irradiation with far-red light of high intensity (Hendricks, Toole, Toole, Borthwick, 1959). Individual species of the family Bromeliaceae and of the genuses Lepidium and Pinus possess different

sensitivity to red light on the part of the seeds (Toole, Toole, Borthwick, Hendricks, 1955; Downs, 1964; Jacopi, 1964). The reaction of a plant and of its individual parts to light is determined to a considerable degree by their age. Already in 1941 Went who studied the effect of light of differing quality on pea seedlings (Went, 1941) established that light (with particular effectiveness in the region of 600-700 millimicrons) intensifies the growth of leaves, suppresses the growth of the first internodes, and stimulates the growth of the succeeding internodes. Thomson (Thomson, 1954, 1959; Thomson, Miller, 1961, 1963) considers, however, that the suppression of the growth of the internodes under the effect of red light is an apparent occurrence and is caused, in essence, by the acceleration of the passage of the cells through the separate phases of growth -- division, stretching, differentiation. Actually, anatomical investigation has shown that under red light there is a decrease in the dimensions of the cells of all tissues of the internodes of the pea and an increase in their transition to differentiation. Contraction of the period of growth of each internode leads to an increase in the number of internodes in pea seedlings under the influence of red light (Downs, Cathey, 1960).

Within the limits of the hypocotyl the differences in the age of the tissues also determine the sign of their reaction to light. In lettuce red light stimulates the growth of young segments (close to the cotyledons) and suppresses the growth of the older segments of the hypocotyl, mainly as a result of the stretching of the cells (Hácker, Hartman, Mohr, 1964). The changes of the growth cone in response to light stimulation received by a leaf depend on the age of the entire plant. In young cocklebur plants red light causes excitation of the growth of the axillary buds; in more mature plants it retards floral initiation (Bogorad, McIlrath, 1960). In the Pharbitis nil irradiation affects floral initiation both in the case of seedlings and also in the case of mature plants; however, in seedlings in the case of irradiation in the middle of the dark period red light and far-red light suppress flowering, whereas in mature plants the suppressing action of red light is removed by far-red light (Nakayama, Borthwick, Hendricks, 1960).

How should one approach an explanation of the action of light through phytochrome if one has in mind not only the different nature of the reactions which are regulated by it but also the different sign and nature of the response to the influence, depending on the species and even the variety which is involved and in one and the same plant, depending also on the age?

Now the opinions of all the researchers amount to one and the same thing -- phytochrome cannot act directly on these various reactions; there should be some kind of general initial stage through which the light stimulus which has been received by the phytochrome has passed. Theoretically it is possible to present the following kinds of action of phytochrome: 1) through the endogenous growth stimulant; 2) through the common element in metabolism; 3) through the system of regulation

which is common for all reactions.

The concept of the action of light through endogenous growth stimulants which was expressed for the first time by Liverman and Bonner (1953) is most deceiving since it equates the problem of studying the mechanism of the action of phytochrome to the determination of the change of the content of phytohormones under various conditions of illumination. The experimental data which have been accumulated in recent years provide a very probable hypothesis with respect to the action of the growth stimulants through the system of regulation (Osborn, 1956; see also the article by V.V. Polevoy in the present book). The most valuable in this respect are the works of Varner (Varner, 1964; Varner, Chandra, 1964) on the induced synthesis of alfa-amylase in germinating seeds of barley under the action of gibberellic acid and also the data of Nooden and Thimann (1965) on blocking by chloramphenicol simultaneously and in equal measure with respect to the growth and synthesis of protein caused by indoleacetic acid in the tissues of the coleoptile of oats, stem of peas, and the tuber of the Jerusalem artichoke. In our subsequent description we will atempt by comparing the action of phytochrome and growth stimulants to determine whether it is possible to explain the action of light on morphogenesis on the basis of its effect on the system of regulation through change in the content of endogenous growth stimulants.

A second point of view -- on the action of phytochrome through a common element in the metabolism -- is held by Borthwick and Hendricks (Hendricks, 1960, 1963; Borthwick, Hendricks, 1960, 1961; Hendricks, Borthwick, 1963). According to their hypothesis the active form of phytochrome which is formed from the inactive form as a result of the absorption of red light in accordance with the scheme

$$PH_2 + R \underset{\text{far red light}}{\overset{\text{red light}}{\rightleftarrows}} P + RH_2$$

constitutes an enzyme -- the dehydrogenase of acetylcoenzyme A. The authors came to this idea on the basis of a study of the biosynthesis of anthocyanins in which acetylcoenzyme A plays a vital role and is the common element which connects the biosynthesis of anthocyanins with the exchange of lipids. Confirmation of this hypothesis, in the opinion of Borthwick and Hendricks, would explain the influence of phytochrome not only on the biosynthesis of anthocyanins but also on the germination of seed (through the stimulation of the break down of fats) and on flowering (through the stimulation of the synthesis of sterols -- the assumed hormones of flowering). However, as yet there are no facts which directly show the effect of light on acetylcoenzyme A. However, even if they were obtained, it would hardly be possible to consider that the mechanism of the action of phytochrome had been explained; still completely unexplained would be the effect of phytochrome on a series of other reactions, especially on the growth of the stem organs and leaves. In addition, the single action of phytochrome on a certain element of the metabolism could not explain the relationship between the sensitivity

to light and the age and species adherence of the plants. However, the study of the effect of light on metabolism through the phytochrome is already beginning to give valuable results which will be examined below.

The idea of the effect of light through a system of regulation has been expressed in some form or another over the course of many years by Mohr. At first he spoke of a radical change of the course of the metabolism in a plant (Mohr, 1960). In recent works Mohr (Hock, Mohr, 1964; Mohr, 1965) is more specific in naming the point of application of the action of phytochrome -- this being potentially active genes, the activity of which also establish the specificity and diversity of the reactions which are observed upon the illumination of plants. In the opinion of Mohr, all cells of a given plant have the same genotype; however, in cells of different types various parts of this genotype are active. In connection with this he distinguishes: 1) inactive genes; 2) active genes which function in the same way in darkness and under light; 3) potentially active genes, the activity of which is excited upon illumination with red light through the phytochrome. Of course, the idea which Mohr has expressed still remains purely hypothetical. It is known, it is true, that far-red light increases the number of chromosome aberrations which occur under the influence of x-rays, while red light removes this effect (Withrow, Moh, 1957; Moh, Withrow, 1959). However, this is an extreme case. It is possible to visualize that the light which has been absorbed by the phytochrome itself has a milder physiological effect on the genes, although this could be certainly not the genes themselves but rather one of the components of the complex system of cell regulation of which we were speaking at the beginning of this article.

Some information which supports these ideas will be examined when we discuss the effect of light on metabolism through the phytochrome.

Let us turn to a discussion of the experimental data which have been obtained upon comparing the effect of light and growth stimulants.

The Interaction of Phytochrome and Growth Stimulants

Below we will examine the effect of growth stimulants (indoleacetic acid, gibberellic acid, and kinetin) on the photomorphogenetic reactions which are connected with the vegetative growth of plants: on germination, the growth of axial organs, and the growth of leaves. The role of growth stimulants in the induction of floral initiation requires special discussion.

Phytochrome and Indoleacetic Acid

In comparing the effect of phytochrome and indoleacetic acid on the processes of morphogenesis the picture which emerges is extremely varied. On the one hand, indoleacetic acid has hardly any effect on

the germination of seeds and on the growth of leaves, both of which are clearly stimulated by phytochrome. On the other hand, phytochrome has a suppressing effect on the growth of epicotyls and hypocotyls of bean seedlings and also on the formation of bending at the top of the hypocotyl, both of which are stimulated by indoleacetic acid. The effect of phytochrome on the growth of the coleoptile of cereals which serves as a test object for the determination of indoleacetic acid is not a single value thing -- the growth of the coleoptile of oats is intensified upon the use of red light (Liverman, Bonner, 1953; Blaauw-Jansen, 1959); the growth of the coleoptile of rice is suppressed (Kefford, 1962). Liverman and Bonner on the basis of stimulation of the growth of the coleoptile of oats which they detected both before and after treatment with far-red light expressed the hypothesis that red light causes the formation of a receptor which is necessary in complex for the activity of endogenous indoleacetic acid. The authors considered that this hypothesis was applicable with respect to the antagonistic action of red light and far-red light on other processes as well, including flowering, the germination of seeds, and the growth of leaves. In other words, in all cases it was assumed that there was a single kind of action by indoleacetic acid and light. Obviously, at the present time this hypothesis should be rejected in its initial form because of two basic reasons. First of all, it has been shown experimentally that red light causes not an increase but rather a reduction in the content of free indoleacetic acid in the coleoptiles of cereals (Blaauw-Jansen, 1959; Phillips, Vlitos, Cutler, 1959; Briggs, 1963). In addition, as has been pointed out, red light and indoleacetic acid act on different aspects of morphogenesis in by no means the same way. The antagonistic action of indoleacetic acid and phytochrome was demonstrated with particular clarity by Klein et al. (Klein, Withrow, Elstad, 1956; Klein, 1959) in tests with isolated hypocotyls of bean seedlings. Red light causes straightening of the hook of the hypocotyl as a result of the intensified stretching of the cells of the concave side; indoleacetic acid causes its formation. In the case of joint action indoleacetic acid reduces the effect of red light in proportion to its concentration in the solution. Klein considers the straightening of the hook of the hypocotyl to be a more specific reaction of photomorphogenesis, inasmuch as it is caused exclusively by the action of red light. The latter cannot be replaced by any of the tested growth stimulants.

On the basis of the results of the study of the effect of light on the growth of segments of epicotyls in solutions of indoleacetic acid of various concentrations Galston (Galston, Hand, 1949; Galston, Baker, 1953) came to the conclusion that red light reduces the sensitivity of segments to indoleacetic acid.

These results were confirmed by Hillman (1959) in tests with internode sections of peas (a more precise difference was observed in calculating the length but not the wet weight). Indoleacetic acid did not remove the suppressing effect of red light on the growth of the segments all the way to a concentration of 10^{-6}M. In a higher con-

centration indoleacetic acid prevented the action of red light. Unfortunately, it is still not clear as to the effect of red light on the concentration of endogenous indoleacetic acid in such segments.

Before undertaking a comparison of the effect of red light and indoleacetic acid on whole bean seedlings, it should be noted that light causes intensification of the growth of leaves and suppression of the growth of the first internodes.

Spraying the pea seedlings with a solution of indoleacetic acid (10 mg/liter) causes only slight weakening of the suppressing action of red light (Vlitos, Meudt, 1957).

In studying the effect of light on auxin metabolism in pea and bean seedlings, Hillman and Galston (1957) found that in the top buds in which the growth is stimulated by light (on account of the leaves) red light causes a lowering of the activity of the oxidase of indoleacetic acid as a result of an increase in the content of the inhibitor. As was shown by subsequent investigations (Galston, 1959), a considerable increase in the content of the inhibitor of the oxidase of indoleacetic acid under light occurs not only in young leaves but also in young internodes of the pea, i.e., in those very parts of the plants where the growth is most strongly inhibited by light. However, importance was not attached to this and the study of the effect of light on the content of the inhibitor was continued.

Inasmuch as the inhibitor was a derivative of kaempferol, the hypothesis arose as to the effect of light on growth through change of the content of flavonoids (Mumford, Smith, Castle, 1961; Furuya, Thomas, 1962; see also Kefeli, 1964).

Having followed the effect of brief irradiation with red light on the growth of a bud and on the accumulation of the inhibitor of the oxidase of indoleacetic acid, Furuya and Thomas (1964) found that the synthesis of the inhibitor begins only after a 4-hour lag period and requires considerably more energy than does the stimulation of the growth of a bud. On this basis the authors came to the conclusion that phytochrome acts on both processes -- the growth of a bud and the synthesis of the flavonoid -- in parallel and not through flavonoids on the growth. According to unpublished data (a letter by Furuya to the Institute of the Physiology of Plants) the latest tests have not confirmed the results which were obtained earlier with respect to the change of the content of derivatives of kaempferol upon illumination.

Perhaps, however, regardless of the change of the content of kaempferol, the lowering of the activity of the oxidase of indoleacetic acid upon exposure to light is still the physiological basis of the photomorphogenetic reactions. Up to the present time it has been necessary to give a negative answer to this question since, in the first

place, single-value changes of the activity of the enzyme upon exposure to light are observed against a background of both suppression of growth and also stimulation of growth and, in the second place, light causes a reduction in the content of indoleacetic acid in the upper parts of bean seedlings (Fletcher, Zalik, 1964) where there is a predominance (in weight) of the leaves and cotyledons, the growth of which is stimulated by light.

Thus, on the basis of the data which has been cited, it is apparently possible to draw still another conclusion -- the action of phytochrome on a plant is not accomplished through indoleacetic acid. The change of the content of indoleacetic acid in a plant under the influence of irradiation with red light occurs in parallel with other morphophysiological changes and is not primary. It is possible that in individual cases indoleacetic acid and phytochrome, if not operating in the same way, in any case act in a similar manner, although there is a lack of specific information on this.

Phytochrome and Gibberellins

The interaction of light and gibberellic acid has been studied in greater detail inasmuch as the greatest activity of both factors is manifested with respect to the same reactions of morphogenesis. On the one hand, gibberellic acid and far-red light cause stimulation, while red light causes suppression of the growth of the stem and hypocotyl in seedlings, while gibberellic acid and red light intensify and far-red light inhibits the growth of the coleoptile of cereals, the growth of leaves, and the germination of light-sensitive seeds.

The question of the connection between the action of gibberellic acid and phytochrome is studied most fully by Lockhart (1956-1964) who defends the idea of the effect of light on growth through the endogenous gibberellins. However, already in the first work by Lockhart (1956) with pea seedlings it was indicated that although gibberellic acid also removes the inhibiting effect of red light on growth, the action of these factors is directed at different stages of growth; treatment with gibberellic acid causes an increase in the total length of the seedling as a result of the stimulation of the growth of the internodes while in the case of the use of red light there is not only the inhibition of the growth of the internodes but also an increase of their number and also stimulation of the growth of leaves. Such results were obtained in tests with seedlings of other plants -- pumpkin, cucumber, sunflower, and beans (Lockhart, 1958a). Subsequently Lockhart showed that upon saturation of pea and bean plants with gibberellic acid (i.e., upon the introduction of exogenic gibberellic acid in an excess amount) they lose the ability to react to red light. On the basis of these data Lockhart expressed the hypothesis that red light causes a reduction in the content of endogenous gibberellins in plants (Lockhart, 1959, 1961; Lockhart, Gottshall, 1959). In one of his later

works Lockhart (1964) found that the sensitivity of the bean stem to red light disappears not only in the case of an excess of gibberellic acid but also upon the removal of the top bud and the leaf which is closest to it. Vlitos and Meudt (1957) reported earlier with respect to the necessity of the hypotetic factor from the upper part for the accomplishment of the stimulating effect of gibberellic acid on the growth of the stem, especially in the case of illumination with red light. In the opinion of Lockhart the predecessor of gibberellin is formed in the upper part; it moves to the stem and is converted there to the active gibberellin which stimulates the growth of the internodes. Red light prevents the formation of gibberellin from the predecessor, which also leads to the suppression of growth. If an excess of exogenic gibberellic acid is added, the effect of red light on growth will not be reflected.

It would seem that the question is clear; it remains only to determine the change in the content of endogenous gibberellins in the case of illumination. The results of the first tests which were conducted with this purpose have not supported Lockhart's hypotheses. In bean seedlings in the case of both etiolated and green plants it has not been possible to find endogenous gibberellins, despite the use of a highly sensitive method (Phillips, Vlitos, Cutler, 1959) in 3-month tobacco plants (of both the short-day and long-day varieties) the content of endogenous gibberellins upon exposure to light increases with the length of the photoperiod (Chaylakhyan, Lozhnikova, 1964). In addition to these data it is possible to cite a series of arguments which refute the hypothesis which was advanced by Lockhart.

Thus, Downs and Cathey (1960) emphasized that gibberellic acid acts on the growth of individual internodes, while red light causes an increase in the number of internodes. In the tests with beans which were described by them red light intensified the effect of gibberellic acid because the stimulating action of gibberellic was conveyed to a larger number of internodes. In tests with green bean plants (all other data which deal with the question apply to etiolated seedlings) gibberellic acid intensified the effect of far-red light, but red light did not remove the effect of gibberellic acid (Downs, Hendricks, Borthwick, 1957).

Sale and Vince (1960) who studied the effect of gibberellic acid on the growth of pea seedlings in the case of their illumination with red light, far-red light, and blue light for periods of time ranging from 15 minutes to 16 hours per day came to a conclusion as to the independence of the action of red light and gibberellic acid. In support of this conclusion they advanced the following proof: 1) in the case of the simultaneous treatment of plants with gibberellic acid and far-red light one can observe the additive nature of their action, i.e., a simple summation of the effect of each treatment; 2) the effect of gibberellic acid on the dwarf variety of peas does not depend on the duration of illumination during the course of a day; 3) gibberellic

acid in high doses partially removes the effect not only of red light but also of blue light as well; 4) in the case of the combined action of red light and gibberellic acid the total length of the plants is the greatest; however, the length of the individual internodes remains less than in the case of treatment with gibberellic acid in the dark

In tests which were conducted by Selman and Ahmed (1962) tomato plants were grown in a 15-hour day with additional brief irradiation with red light or far-red light. The growth of such plants was stimulated by far-red light regardless of the concentration of gibberellic acid which was employed to treat the plants. This applies both to the growth of the stem in length and also to the accumulation of wet weight by the stem and petioles, while at the same time it was not important as to whether the plants were treated with gibberellic before or after their illumination with far-red light.

The results of two works which have only just been examined have fully confirmed the data which were obtained earlier by Hillman (1959) in methodologically stricter tests with isolated segments of the third internode of bean seedlings which were raised in darkness and with the use of red light. The suppression of the growth of segments of dark seedlings does not depend on the presence of gibberellic acid in the medium; the absolute value of the lagging in the growth in comparison with the dark control case is the same for any concentration of gibberellic acid and when it is not used. There is no case in which gibberellic acid does not remove the effect of red light. Far-red light and gibberellic acid act additively on the growth of seedling segments which have been raised under red light and cause stimulation of the growth.

Mohr and Appuhn (1962) raised white mustard seeds in darkness in water and in solutions of gibberellic acid of various concentrations, i.e., they introduced gibberellic acid through the roots and not through the part above the ground. In this case the suppressing action of red light on the growth of the hypocotyl was almost the same when gibberellic acid was not used and when the plants were saturated with gibberellic acid. Judging from the course of the curves which show the relation of the growth to the dose of gibberellic acid, red light does not reduce the effect of the action of gibberellic acid. In addition, gibberellic acid stimulated only the stretching of the cells, while red light inhibited both stretching and division.

Upon the conduct of an experimental check these data were confirmed fully by Nwachuku and Lockhart (1964) who, however, consider that mustard is an unsuitable object for this kind of investigation. The authors consider that in the case of peas and beans the courses of the effect of red light and gibberellic acid on plants are more closely connected with each other than is the case with mustard. However, as is evident from the work by Hillman, this connection is also not manifested in the pea.

As has been shown by tests which were conducted by Roesel and Haber (1963), red light causes intensification of the growth of only the younger apical part of the coleoptile of wheat, but inhibits the growth of the more mature basal part. Gibberellic acid stimulates the growth of all parts of the coleoptile in the same measure, whereas illumination does not influence the sensitivity of the coleoptile to treatment with gibberellic acid.

The red light which is necessary for the growth of sections which have been cut from etiolated bean leaves can be replaced in part by treating them in darkness with gibberellic acid, while the action of the latter is partially removed by far-red light (Scott, Liverman, 1957; Liverman, Johnson, 1958). In addition, both gibberellic acid and red light stimulate not only the stretching but also the division of the cells of the leaf. However, if the segments which have been treated with gibberellic acid are illuminated with red light, the stimulation of division is reduced and, on the other hand, the stimulation of the stretching is intensified still more (Humphries, Wheeler, 1960). Thus, in this case also, like the growth of the stem of seedlings, the total results of the effect of light and gibberellic acid on the plant appear to be the same, however, they apparently are achieved in different ways as a result of the occurrence of different intermediate reactions. It should also be noted that in the work which was cited above by Selman and Ahmud (1962) gibberellic acid hardly acted at all on the growth of the leaves of green tomato plants, whereas far-red light caused considerable stimulation with respect to the increase of the wet and dry weight of the leaf sections.

Particularly great similarity has been detected in the action of gibberellic acid and red light on the germination of seeds. Gibberellic acid causes 100% germination in darkness of light-sprouting seeds of lettuce, Bidens radiata, and Lythrum salicaria, replacing the action of red light. However, far-red light does not remove the stimulating effect of gibberellic acid on germination, and gibberellic acid does not remove the inhibiting effect of far-red light (Kahn, Goss, Smith, 1957; Haber, Tolbert, 1959; Ikuma, Thimann, 1960, 1963a; Rollin, 1964c). Results of this kind were obtained not only with gibberellic acid but also in the case of the use of a mixture of gibberellins A_4 and A_7 which possess still greater activity with respect to stimulating the germination of seeds (Ikuma, Thimann, 1963c).

Partial elimination of the effect of gibberellic acid in the case of illumination of seeds with far-red light has been described only in one of the earlier works (Evenari, Neumann, Blumenthal-Goldschmidt, Mayer, Poljakoff-Mayber, 1958).

Just as red light does so also does gibberellic acid have an effect on the earliest stages of germination; the maximum sensitivity of the seeds to both factors occurs 1½ hours after the beginning of their

wetting with this sensitivity being more expressed in the axial part of the seedling and not in the cotyledons (Ikuma, Thimann, 1960, 1963a). In both cases the mitotic activity at the end of the rootlet does not undergo changes (Haber, Luipold, 1960).

However, in the case of a certain arrangement of the test and the use of a low optimum temperature the effects of gibberellic acid on germination were examined by Haber and Tolbert (1959); they were able to distinguish between the action of gibberellic acid and light and show that the red light-far-red light system can regulate the germination of seeds in the case where the activity of gibberellic acid is blocked. Finally, the weightiest proof of the absence of a single mechanism in the case of the action of gibberellic acid and red light was obtained by Ikuma and Thimann (1960) who established that in germinating lettuce seeds the content of endogenous gibberellins is extremely low and is not increased upon illumination with red light. On the basis of the data which were obtained the authors come to the valid conclusion that gibberellic acid and red light act independently of each other, initiating a chain of chemical reactions with the same end products.

Phytochrome and Kinetin

Already within a year after the discovery of kinetin Miller (1956) directed attention to the similarity of the action of this substance to the action of red light with respect to the germination of seeds, the growth in length of the stem of bean seedlings, and the growth of sections from etiolated bean leaves. However, upon determining that far-red light does not remove the action of kinetin and that the latter acts on the germination with a considerably weaker effect that red light, Miller suggested that light and kinetin influence different aspects of the process of growth.

Soon Hillmann (1957) showed that kinetin can replace red light in the stimulation of vegetative multiplication of duckweed. In the same way as red light, kinetin also stimulates the growth of segments of coleoptiles of oats (Schrank, 1957) and causes intensified synthesis of anthocyanin in isolated petals of balsam (Klein, Hagen, 1961) and in isolated buds of rudbeckia, perilla, and morning glory (Butenko, 1964).

Thus, the sign of the action of kinetin and red light coincides with respect to all processes which are regulated by light acting through phytochrome. The exception is only the hook of the apical part of the hypocotyl of seedlings which, as was indicated above, is a specific reaction of photomorphogenesis. However, more detailed investigations of the interaction of light and kinetin with respect to the germination of seeds and the growth of leaves have shown that also in this case there is not complete congruence in the mechanism of action.

Kinetin in the dark causes slight germination of lettuce seeds of the Grand Rapids variety which are slight according to the data of Miller

(1958) and up to 95% according to the data of Evenari et al. (Evenari, Nenmann, Blumenthal-Goldschmidt, Mayer, Poljakoff-Mayber, 1958). However, in all cases kinetin intensifies the stimulating action of light with respect to germination; far-red light does not remove the action of kinetin. The effect of kinetin and red light can be limited easily by lowering the temperature (to 14-17°) to a point at which kinetin is inactive or causes a delay in germination (Haber, Tolbert, 1959; Weisz, 1960). The action of kinetin with respect to germination is distinguished from the action of red light and gibberellic acid both with respect to time and also with respect to the place of application. At a temperature of 37° only kinetin stimulates the mitotic activity of the end of the rootlet (Haber, Luippold, 1960). At room temperature kinetin suppresses the growth of the root and hypocotyl and strongly stimulates the growth of the cotyledons; however, it does not have an effect on swelling during the course of first 8 hours of the wetting of the seeds, i.e., it does not influence the early phases of germination (Ikuma, Thimann, 1963a). In the opinion of Ikuma and Thimann kinetin acts on the later phases of germination in comparison with red light and gibberellic acid, increasing the sensitivity of the seeds to red light.

In connection with this it would be interesting to determine the effect of red light on the content of endogenous kinins in the seeds during germination. An investigation of this kind was begun by Barzilai and Mayer (1964). Using as the biotest the formation of callus in the isolated pith of a tobacco stem, the authors established that kinins which are absent in quiescent lettuce seeds appear 48 hours after 30-second irradiation with red light. If far-red light is employed following the red light, the seeds remain in a state of quiescence and do not contain kinins. In order to evaluate these results it is necessary to have a more detailed study of the change in the content of kinins under the influence of red light and far-red light over time and to identify these compounds.

In a series of works Liverman et al. (Scott, Liverman, 1956, 1957; Liverman, Johnson, 1958) clearly established that kinetin stimulates the growth of disks from etiolated leaves of dwarf beans, regardless of the illumination; the action of kinetin is not removed by far-red light; in the case of the combined use of kinetin and red light there is an additive effect, i.e., a simple summation of both effects. In the opinion of Liverman, red light and kinetin act on different processes. It is interesting that with respect to the growth of disks from the leaves the same action as with kinetin is manifested by 6-benzylaminopurine and especially by adenine. In connection with this Liverman suggests that adenine or a compound which is close to it could be the final product of the action of red light.

Anatomical study has shown that kinetin causes only stretching of the cells. The data diverge with respect to the action of red light. Powell and Griffith (1960) found that red light, in contrast to kinetin,

acts only on the division of the cells. However, in the case of their combined use the cells achieve greater size than is the case under the action of kinetin alone, i.e., it is possible that there is some mutual effect of these factors. According to the observations of Humphries and Wheeler (1960), red light stimulates both the expansion and also the division of the cells. It is possible that the divergence of the results is connected with differences in the arrangement of the test.

One of the most characteristic properties of kinetin is its ability to prevent a lowering of the content of protein and chlorophyll in isolated leaves. Sugiura (1963) found that red light also acts in the same way. In the case of their combined use red light intensifies the effect of kinetin in low concentrations. It is particularly interesting that the action of red light is removed not only by far-red light but also by 2,4-dinitrophenol, inhibitors of the synthesis of protein (chloramphenicol), analogues of amino acids, and derivatives of nucleic acids. These data led Sugiura to the conclusion that red light, just as kinetin, causes activization of the synthesis of protein. However, kinetin and red light act in an opposite manner on the absorption of tagged P^{32} of an inorganic phosphate; red light stimulates this process, causing the rapid inclusion of P^{32} in the acid-soluble fraction of organic phosphates, while kinetin inhibits the absorption of P^{32}.

Thus, even in the case of deep similarity in the mechanism of the action of kinetin and red light which includes the most important aspects of metabolism, full analogy is not observed.

Taken together, the data which have been cited do not provide a basis for a conclusion with respect to the action of light on photomorphogenesis through a change in the content or activity of endogenous growth stimulants such as indoleacetic acid, gibberellins, and kinetins. If such changes do exist, they apparently occur in parallel with growth reactions and are not their only cause.

Hillman (1959) denies the role of growth stimulants in photomorphogenesis, considering that red light suppresses only "endogenous" growth and does not affect the growth which is caused by the action of growth stimulants.

An opposite opinion continues to be held by Liverman (1959) who suggests that auxin, gibberellic acid, and purines (kinins) are included at some stage in the branched chain of the reactions which lead to morphogenesis from the absorption of light.

It seems to us that it would be more probable that endogenous growth stimulants and light operate independently from each other but that the courses of their action on morphogenesis are so varied and complex that they almost coincide with respect to some reactions while

strongly diverging with respect to other reactions.

Mention should also be made of the results of a study of the effect of light on the content in plants of physiologically active substances which have not yet been identified. Thus, in leaf peduncles of spiderwart in the case of the action of red light there is a decrease not only in the content of the total auxins but also in the content of substances of the bios group (Ruge, 1953, 1960). Judging from the histograms which were obtained by Hahn (1959), in various plants depending on their age at the time of illumination with light of various spectral compositions there is a change in the content of individual unidentified auxins. In the case of the illumination of etiolated pea seedlings with red light the change in the total content of auxins corresponds approximately to the change in the intensity of growth (Phillips, Vlitos, Cutler, 1959). The authors consider that one of these substances which experiences the greatest changes is similar to indoleacetic acid, while the composition of the other substances remains unknown.

Blaauw-Jansen (1959) isolated a substance from the upper part of the coleoptiles of oats which he called the "red light factor." This substance which is formed upon irradiation of the coleoptiles with red light in the presence of low concentrations of indoleacetic acid causes the same stimulation of the growth of the coleoptiles as does their irradiation with red light. The substance does not possess any activity along the line of that of the gibberellins.

In order to explain the results which were obtained upon the study of the interaction of light and gibberellic acid in tests with dwarf peas Simpson and Wain (1961) advance the hypothesis of the formation, under the influence of light, of a growth inhibitor at the top of the seedling.

It would be interesting from this point of view to study the influence of the brief illumination of plants with red light with respect to the content in them of growth inhibitors of the type of those phenol compounds which have been detected in suckers found on trees when they enter under the influence of a long day during the period of quiescence (Sarapuu, 1964, 1965; Robinson, Wareing, 1964; Eagles, Wareing, 1964).

Thus, among the physiologically active substances there is not yet a compound which has been found which could be considered to be the primary product which is formed upon the activation of phytochrome by light energy. At the same time the presence of such a substance (or substances) is confirmed by observations of the rapid transfer of light stimuli in tissue, for example, in the case of irradiation of one side of a lettuce seed with red light and of the other side with far-red light or in the case of irradiation of part of a wheat leaf with red light (Klein, Preiss, 1958; Wagne, 1964).

Let us now turn to the results of the biochemical study of the changes which are caused by light; the basic purpose of this examination is to determine the primary elements of metabolism which are common for the various reactions of photomorphogenesis.

The Effect of Phytochrome on Metabolism

Respiration and Oxidative Phosphorylation

Experimental investigations of the common element in metabolism which is affected by phytochrome have been directed above all at the processes of respiration and oxidative phosphorylation as the source of the energy which is necessary for all the reactions of photomorphogenesis. Actually, the intensity of respiration of light-sensitive lettuce seeds is increased upon irradiation with red light (Hagen, Borthwick, Hendricks, 1954; Evenari, Neumann, Klein, 1955; Nyman, 1963). This also agrees with the observation by Ikuma and Thimann (1964) with respect to the necessity of aerobic conditions for the post-induction phase of germination which occurs immediately after brief irradiation of the seeds with red light.

However, not all the tissues and organs of a plant react to red light with intensified respiration. The sign of the action of red light on respiration is identical to the sign of its action with respect to the corresponding stage of morphogenesis (Leopold, Guernsey, 1954); it causes an increase of respiration in the leaves of long-day plants (barley) and in lettuce seeds, but inhibits the respiration of leaves of short-day plants (soybean and cocklebur), of the mesocotyl of oats, and of the stem of peas. In all cases far-red light removes the effect of red light. Consequently, respiration cannot be the common element which reacts in the same way to the action of phytochrome.

In tests by Hock and Mohr (1964) with mustard seedlings red light stimulated the respiration of the cotyledons which experienced intensified growth in this case and also stimulated the respiration of the hypocotyls for which growth was inhibited.

However, the change of respiration was observed not earlier than one to two days after irradiation, therefore, it cannot have a direct relation to the mechanism of the primary action of phytochrome.

The data with respect to the influence of phytochrome on oxidative phosphorylation are contradictory. Gordon and Surrey (Gordon, Surrey, 1958, 1960; Gordon, 1964) found that the irradiation of etiolated seedlings of oats with red light leads to intensification of oxidative phosphorylation in the mitochondriae which come from the coleoptile. Red light also stimulates the absorption of P^{32} from inorganic phosphate by germinating lettuce seeds and its inclusion in the acid-soluble and phospholipid fractions of phosphoroorganic compounds (Surrey, Gordon, 1962; Surrey, 1962).

However, Sisler and Klein (1961) did not confirm these data and did not detect changes of the content of ATP and of the speed of inclusion of tagged phosphate in organic phosphates and nucleotides of seedlings of beans and oats under the influence of red light and far-red light.

In his work which was cited above, Sugiura (1963) in accordance with the data Gordon and Surrey observed the stimulating action of red light with respect to the absorption of inorganic phosphate and its inclusion in the acid-soluble fraction of phosphoroorganic compounds in disks from tobacco leaves. Apparently it is necessary to further clarify the influence of red light on oxidative phosphorylation.

Anthocyanins

The synthesis of anthocyanins in a plant under the action of light is related to certain stages of the morphogenesis of plants. Mention was made above of the accumulation under red light of anthocyanins in a series of plants (bean, mustard, turnip, red cabbage, sorghum). The same phenomenon is observed in rye seedlings (Metche, Gay, 1964). The anthocyanic coloration of young, growing leaves of cedar and oak is well known. In the case of lupine the varieties with anthocyanic coloration are distinguished by their speed of growth and by their early maturation (Maysuryan, Tyutyunnikov, 1962).

In isolated roots of Chrysanthemum leucantheum which are raised in vitor the anthocyanic coloration appears strictly at the same time as the beginning of growth -- 18 hours after the extraction of the root from the seed (Beguin, 1964). In growing isolated hypocotyls of balsam in the light under sterile conditions in the presence of sugar, Arnold and Alston (1961) found that the 5-mm segment closest to the cotyledon is characterized by the greatest magnitudes of the intensity of growth, of respiration, and of the content of anthocyanins. These results gave the authors a basis for considering the formation of anthocyanins to be an indicator of the processes of exchange which accompany differentiation.

The connection between the biosynthesis of anthocyanin and respiration was studied earlier by Eberhardt (1954) for the most varied objects -- seedlings of red cabbage, fall leaves of Saxifraga crassifolia and Partenocissus vitacea, and maturing fruits of Sorbus hybrida. In tests with isolated leaves of Saxifraga the synthesis of anthocyanins and respiration are intensified under light in the presence of sugar and are suppressed by iodoacetic acid. At the same time, 2,4-dinitrophenol intensified respiration but suppressed the synthesis of anthocyanin in the same way as it occurs with growth and other processes which require a sufficient amount of energy. These data led Eberhardt to the idea that anthocyanins are formed in the presence of intensified metabolism, especially in the case of the accumulation of compounds which are rich in energy due to oxidative phosphorylation.

In studying the role of ATP in the stimulating effect of red light of

high energy on the biosynthesis of anthocyanin, Kandeler (1960) obtained clearly positive results. In his tests with red cabbage seedlings the action of the light to a certain extent was fulfilled in the feeding of the plants with saccharose, ATP, and ascorbic acid, but not by the predecessors of anthocyanins (sodium acetate, phloroglucinol, shikimic acid, and L-phenylalanin). In the opinion of Kandeler it is ATP and not the predecessors which is the limiting factor in the biosynthesis of anthocyanin and which is removed by light. On the other hand, in the case of rye seedlings light caused intensification of the inclusion of phenylalanin-3-C^{14} in anthocyanic pigments (Metche, Gay, 1964).

Thus, there is still an unsolved problem with respect to which element in the process of the biosynthesis of anthocyanins is affected by light; however, in any case its action is not primary, inasmuch as it is reflected only after a lag period of not less than 6 to 8 hours (Siegelman, Hendricks, 1958b; Klein, Withrow, Elstad, and Price, 1957).

Thimann and Radner (1955a, 1955b) discovered that in duckweed (Spirodela oligorrihiza) the photochemical reaction of the formation of anthocyanins is suppressed by ethionin and the antimetabolites of nucleic exchange, especially 8-asaguanine. The metabolites remove the suppression which is caused by the antimetabolites. The authors hypothesize that the light reaction of the biosynthesis of anthocyanins is connected with the synthesis of nucleotides and nucleic acids.

This idea is supported by the data of Arnold and Albert (1964) who studied the biosynthesis of anthocyanin in isolated segments of the hypocotyl of balsam. 8-Asaguanine suppressed not only the synthesis of anthocyanin under light but also the growth of the segments. However, the antimetabolite had almost no effect on the youngest segments which consisted of meristomatic tissue (as was indicated above, this part of the hypocotyl reacts to red light not with inhibition but rather with intensification of growth).

It is known that the content, composition, and distribution of anthocyanins in plants are under strict genetic control (Alston, 1959). Hess (1964) in tests with the petunia was able in the petals of the flowers to cause suppression of the genetically based synthesis of anthocyanins by means of the introduction of 2-thiouracil into the flower buds during the appropriate period of their development. In accordance with the hypothesis of Hess, the appearance of anthocyanin in the flowers is preceded by the formation of the corresponding informational RNA.

The data which we have at our disposal undoubtedly are insufficient for the conclusion that light acts on the synthesis of anthocyanin through a system of regulation which includes informational RNA; however, the data are also fully in agreement with such a conclusion. Apparently only in this way is it possible to explain the following interesting

facts which are contradictory to the idea of the association of the biosynthesis of anthocyanins with periods of intensive morphogenesis and metabolism.

In the case of Perilla ocymoides and P. nankinensis the photoperiodic induction by a short day leads to a sharp reduction in the content of anthocyanins in the leaves (Yermolova, Shcheglova, 1948). The same stage of morphogenesis is accompanied in another short-day plant -- Kalanchoe blossfeldiana -- by stimulation of the synthesis of anthocyanin (Neyland, Ng, Thimann, 1963).

According to the data of Stafford (1956), in an isolated first internode of sorghum the synthesis of flavonoids being stimulated by light is localized not only in young segments, as in the case of balsam, but, on the contrary, in tissues which have completed their growth. In this work another point which is notable is the indication as to the necessity of illumination for the synthesis of flavonoids (luteolin) the composition of which contains a B ring which has hydroxyl groups at the 3 and 4 positions, i.e., the part of the molecule of anthocyanin for which synthesis is precisely regulated by genome, in particular in the petunia (Hess, 1964).

Chlorophyll

In describing the history of the study of phytochrome we mentioned the stimulating effect of red light on the synthesis of chlorophyll. The objects which were studied were leaves of etiolated seedlings of beans, wheat, and garden peppergrass (Klein, Withrow, Elstad, and Price, 1957; Price, Klein, 1961; Virgin, 1957, 1958; Mitrakos, 1961). The plants were irradiated for several minutes with red light and then were put in darkness for several hours, after which a study was made of the synthesis of chlorophyll in white light. In such an arrangement of the red light reduces the lag period of the appearance of chlorophyll a and protochlorophyll a upon the use of light (Virgin, 1958). The synthesis of chlorophyll is also intensified as a result of the prolonged (22 hours) preliminary irradiation of bean seedlings with far-red light (Margulies, 1965).

Recently Lebedev and Litvinenko (1965) published the results of a study of the synthesis of chlorophyll by etiolated corn seedlings directly in the case of the use of brief (up to 60 minutes) illumination of them with red light (660 millimicrons) and far-red light (770 millimicrons) of low intensity. Under red light chlorophyll is formed, whereas under far-red light only protochlorophyllide is formed. The authors consider that red light is necessary for the conversion of protochlorophyllide into chlorophyllide a, which is the immediate predecessor of chlorophyll a. Apparently this occurs as a result of the absence of the appropriate enzyme.

Proteins and Enzymes

The study of the effect of light which has been absorbed by phytochrome on the synthesis of proteins and enzymes in plants is only beginning. At the same time the determination of this aspect of the action of light is particularly important, inasmuch as the induced synthesis of protein and the synthesis of protein "de novo" represent one of the weightiest proofs of the participation of the system of regulation in the mechanism of photomorphogenesis.

Marcus (1960) discovered that red light of weak intensity which has been absorbed by phytochrome causes synthesis in etiolated bean seedlings of the enzyme which is connected with NADP and which catalyzes the oxidation of glyceraldehyde-3-phosphate to 1,3-diphosphoglyceric acid. Like other reactions which are regulated by phytochrome, brief irradiation with red light and prolonged irradiation with far-red light had the same effect (Margulies, 1965).

The synthesis of the enzyme is not suppressed by chloramphenicol which, according to the data of Margulies (1964), is a selective inhibitor of the synthesis of specific proteins. Apparently it is these very properties of chloramphenicol which also explain the insensitivity to it of another reaction which is regulated by phytochrome -- straightening the bend of isolated hypocotyl of bean seedlings (Margulies, 1962).

In studying the biochemical changes which are connected with the activity of phytochrome Price, Mitrakos, and Klein (1964) discovered that in etiolated leaf segments of corn brief irradiation with red light causes intensification of the breakdown of starch and sugar. Far-red light acts antagonistically. These changes occur parallel to the photomorphogenetic reaction -- the intensification of the growth of leaf segments. Unfortunately, the activity of the corresponding enzymes was not determined.

Interesting data were obtained upon studying the action of light in connection with the germination of seeds. According to the observations of Ikuma and Thimann (1963c), brief irradiation of lettuce seeds causes breakdown of the endosperm, which is a necessary condition for the root to emerge beyond the limits of the seed-coats. Disturbance of the integrity of the endosperm makes it insensitive to red light. The injection into the seed of enzymes which can facilitate the breakdown of the endosperm -- cellulases, pectinases, and pentosanases -- causes almost 100% germination of the seeds in the dark. The absence of change of the activity of these enzymes in the seed under the influence of phytochrome is explained by the authors as a lack of refinement of the method which does not catch quantitatively slight shifts in the activity of the enzymes which, however, are important in their nature. Ikuma and Thimann suggest that the action of the light through the phytochrome is directed at the hydrolytic enzymes of the endosperm. Up to the present

time there is no other information with respect to the effect of light on these enzymes.

At later stages of germination in one and two-day seedlings it has been possible to detect the stimulating effect of the light which was absorbed by the phytochrome on the synthesis of protein. In tests which were conducted by Landgraf (1961) red light caused an increase in the content of protein in white mustard seedlings. Far-red light removed the effect of red light in the case of brief irradiation; in the case of continuous irradiation it also caused stimulation of the synthesis of protein (in the same way as this is observed with the reactions of morphogenesis). The increase in the content of protein occurred not only in the cotyledons but also in the roots and the hypocotyls, i.e., in organs not having reserve nutrients. Landgraf considers that the stimulation of the synthesis of protein which is caused by red light is not a side reaction but rather the cause of morphogenetic changes. In his last survey article devoted to the effect of light on morphogenesis Mohr (1965) mentions that he detected intensification of the synthesis of protein and RNA in mustard seedlings in response to the use of red light. However, he does not furnish any numerical data.

In plants, just as in other organisms, the first stage of the biosynthesis of protein is the activation of aminoacids by means of joining them to the carrier form of RNA ro an RNA carrier (Webster, 1961). Henshall and Goodwin (1964) showed that during the germination of pea seeds the activity of the enzyme which activates amino acids increases primarily due to the synthesis of this enzyme. Brief irradiation of four-day etiolated seedlings with red light caused tow reactions which proceeded in parallel with each other -- an increase of the activity of this enzyme in the leaves (also, apparently, due to synthesis "de novo") and a build-up of the dry weight by the leaves (the first sample was taken 24 hours after irradiation). Far-red light removed the effect of red light.

The small number (and in some cases contradictory) results of the study of changes of metabolism under the influence of light which has been absorbed by phytochrome make it possible to draw only preliminary conclusions. Apparently respiration is not the common element at which the action of light is directed. Inasmuch as the sign of the change of respiration coincides with the sign of the change of the intensity of the growth processes, it is possible to think that both changes occur only after "radical switching of the metabolism" (according to the terminology of Mohr). The contradictory data on the effect of light on oxidative phosphorylation require additional checking.

In the study of the effect of light on the biosynthesis of anthocyanins there unfortunately were no investigations of enzymes which could play the role of a linking element between the different ways of exchange (in the same way that this is suggested by the Beltsville researchers with respect to the acetylcoenzyme A). However, the close connection of

the biosynthesis of anthocyanins with the reactions of morphogenesis and its direct relation, like these reactions, to the system of regulation make the biosynthesis of anthocyanins a suitable object for the investigation of the mechanism of the action of light on plants.

The effect of red light on the synthesis of chlorophyll and on the breakdown of carbohydrates is probably based on its action on the corresponding enzymes, although up to the present time the action has remained unexplained.

The synthesis, under the influence of red light, of the enzyme which activates amino acids during the germination of seeds and the synthesis of protein in seedlings which are being subjected to red light correspond fully with the hypothesis on the action of the light which has been absorbed by phytochrome on morphogenesis through a system of regulation.

Conclusion

In summarizing that which has been said, it should be emphasized first of all that the experimental material which is at our disposal is clearly inadequate for a more or less precise understanding of the mechanism of the action of phytochrome. Of the three hypotheses on the mechanism of the action of phytochrome (by means of growth stimulants, by means of a common link in the metabolism, and by a system of regulation) the one which is apparently closest to the truth is the third one which speaks of the action of light which has been absorbed by phytochrome through a system of regulation which includes active, specific DNA and RNA. In support of this concept it is now possible to cite not only information on the diversity, specificity, and genotypic dependence of the reactions of the plants and their individual organs on light and information concerning change of sensitivity to the action of light during the course of ontogenesis, but also the first data on the "de novo" synthesis of proteins and enzymes under the action of red light.

If one returns to the scheme of Bopp, then it is evidently necessary to admit that the entire course from phytochrome to the system of regulation remains a puzzle. Growth stimulants of the type of indoleacetic acid, gibberellin, and kinetin act on this system and through it act on morphogenesis, perhaps in ways which are also close, but still in different ways.

In studying the possibilities for the transmission of external influences on some elements of the system of regulation and in seeking out these sensitive elements the use of phytochrome as the acceptor of light stimulation should, ~~as it seems~~ to us, play a significant role.

BIBLIOGRAPHY

1. Butenko, R.G. 1964. Kul'tura izolirovannykh tkaney i fiziologiya morfogeneza rasteniy (A Culture of Isolated Tissues and the Physiology of the Morphogenesis of Plants). Moscow, Science Publishing House.

2. Yermolayeva, Ye.Ya., Shcheglova, O.A. 1948. "Anthocyan and the Development of Plants." Doklady AN SSSR (Reports of the Academy of Sciences of the USSR), 60, 5, 901-903.

3. Katunskiy, V.M. 1937. "The Relation of the Photoperiodic Reaction of Plants to the Spectral Composition of Light." Ibid., 15, 8, 501-504.

4. Kefeli, V.I., Turetskaya, P.Kh. 1964. "The Mechanism of the Action of Natural Inhibitors of the Growth of Plants." Uspekhi sovr. biol. (Progress of Modern Biology), 57, 1, 99-114.

5. Kleshin, A. 1946. "The Significance of the Spectral Composition of Light for Photoperiodic and Form-Establishing Processes during Various Phases of Development." Doklady AN SSSR (Reports of the Academy of Sciences of the USSR), 52, 9, 819-822.

6. Lebedev, S.I., Litvinenko, L.G. 1965. "The Biosynthesis of Chlorophyll in the Red and Near Infrared Regions." Ibid., 160, 6, 1427-1429.

7. Maysuryan, N.A., Tyutyunnikov, A.I. 1962. "Anthocyanic Coloration as a Sign in the Case of Selection for Rapid Growth and Early Maturity." Izvestiya TSKhA (News of the Timiryazevskaya Agricultural Academy), 3 (46), 59-65.

8. Sarapuu, L. 1964. "Phlorizin as an Inhibitor and the Seasonal Dynamics of the Products of Its Metabolism in Apple Tree Shoots." Fiziologiya rasteniy (The Physiology of Plants), 11, 4, 607-614.

9. Sarapuu, L.P. 1965. "The Physiological Action of Phloridzin as an Inhibitor during Growth and at Rest in .e Apple Tree." Fiziologiya rasteniy (The Physiology of Plants), 12, 1, .34-145.

10. Khendriks, S. 1964. "The Speed of the Conversion of Phytochrome as the Basic Factor Which Determines the Photoperiodic Reaction of Plants." In the collection: Biologicheskiye chasy (Biological Clocks), Moscow, World Publishing House.

11. Chaylakhyan, M.Kh., Lozhnikov, V.N. 1964. "Photoperiodism and the Dynamics of Gibberellins in Plants." Fiziologiya rasteniy (The Physiology of Plants), 11, 6, 1006-1014.

12. Shakhov, A.A., Khazanov, V.S., Stanko, S.A. 1965. "The Spectral Light-Absorbing Capacity of the Leaves of the Crown of a Tree." Fiziologiya

rasteniy (The Physiology of Plants), 12, 1, 22-26.

13. Aghion, J., Jouglard, C., Lourtioux, A. 1962. "Effects d'clairements colores de faibles energies sur la croissance de coleoptiles d'avoines in vitro." Physiol. plantarum, 15, 3, 452-456.

14. Alston, R.E. 1959. "Physiology and the Inheritance of Anthocyanin Pattern." Genetica, 30, 261-277.

15. Arnold, A.W., Albert, L.S. 1964. "Chemical Factors Affecting Anthocyanin Formation and Morphogenesis in Cultured Hypocotyl Segments of Impatiens Balsamina." Plant Physiol., 39, 3, 307-312.

16. Arnold, A.W., Alston, R.E. 1961. "Certain Properties of Hypocotyl of Impatiens Balsamina Reflecting Physiological Complexity." Plant Physiol., 36, 5, 650-656.

17. Barsilai, E., Mayer, A.M. 1964. "Kinins in Germinating Lettuce Seed." Austral. J. Biol. Sci., 17, 3, 798-800.

18. Beguin, F. 1964. "Contribution a la localisation de la biogenese des pigments anthocyaniques du meristeme de la coiffe de Chrysanthemum leucanthemum L. par le methode de culture d'organes in vitro." Ber. Schweiz. bot. Ges., 74, 267-276.

19. Blaauw, O.H. 1961. "The Influence of Blue, Red and Far-Red Light on Geotropism and Growth of the Avena Coleptile." Acta bot. neerl., 10, 3, 397-450.

20. Blaauw, O.H. 1963. "Effects of Red Light on Geotropism of Avena and Their Possible Relations to Phototropic Phenomena." Acta bot. neerl., 12, 4, 424-432.

21. Blaauw-Jansen, G. 1959. "The Influence of Red and Far-Red Light on Growth and Photoropism of the Avena Seedling." Acta bot. neerl., 8, 1, 1-39.

22. Bogorad, L., McIlrath, W.J. 1960. "Effect of Light Quality on Axillary Bud Development in Xanthium." Plant Physiol., 35, Suppl., XXXII.

23. Bonner, J. 1959. "Protein Synthesis and the Control of Plant Processes." Amer. J. Bot., 46, 1, 58-62.

24. Bopp, M. 1962.(1963). "Über die innere Steuerung der Morphogenese bei höheren Pflanzen." Ber. Dtsch. bot. Ges., 75, 11, 64-67.

25. Borthwick, H.A. 1964. "Phytochrome Action and Its Time Displays." Amer. Naturalist, 98, 902, 347-356.

26. Borthwick, H.A., Cathey, H.M. 1962. "Role of Phytochrome in Control of Flowering of Chrysanthemum." Bot. Gaz., 123, 3, 155-162.

27. Borthwick, H.A., Hendricks, S.B. 1961. "Effects of Radiation on Growth and Development." In: Handbuch der Pflanzenphysiologie, Bd. 16, S. 299-330.

28. Borthwick, H.A., Hendricks, S.B., Parker, M.W. 1948. "Action Spectrum for Photoperiodic Control of Floral Initiation of a Long-Day Plant: Winter Barley (Hordeum Vulgare)." Bot. Gaz., 110, 3, 103-118.

29. Borthwick, H.A., Hendricks, S.B., Parker, M.W. 1952. "The Reaction Controlling Floral Initiation." Proc. Nat. Acad. Sci. USA, 38, 11, 929-934.

30. Borthwick, H.A., Hendricks, S.B., Parker, M.W., Toole, E.H., Toole, V.K. 1952. "A Reversible Photoreaction Controlling Seed Germination." Proc. Nat. Acad. Sci. USA, 38, 8, 662-666.

31. Borthwick, H.A., Hendricks, S.B. 1960. "Photoperiodism in Plants." Science, 132, 3435, 1223-1228.

32. Borthwick, H.A., Downs, R.J. 1964. "Roles of Active Photochrome in Control of Flowering of Xanthium Pensylvanicum." Bot. Gaz., 125, 4, 227-231.

33. Briggs, W.R. 1963. "Red Light, Auxin Relationships and the Phototropic Response of Corn and Oat Coleoptiles." Amer. J. Bot., 50, 2, 196-207.

34. Briggs, W.R., Siegelman, H.W. 1963. "Phytochrome Distribution in Etiolated Seedlings." Plant Physiol., 38, Suppl., V.

35. Butler, W.L. 1964. "Dark Transformations of Phytochrome in Vivo." Quart. Rev. Biol., 39, 1, 6-10.

36. Butler, W.L., Lane, H.C. 1965. "Dark Transformations of Phytochrome in Vivo. vo. II." Plant Physiol., 40, 1, 13-17.

37. Butler, W.L., Lane, H.C., Siegelman, H.W. 1963. "Non-photochemical Transformations of Phytochrome in Vivo." Plant Physiol., 38, 5, 514-519.

38. Butler, W.L., Norris, K.H., Siegelman, H.W., Hendricks, S.B. 1959. "Detection, Assay and Preliminary Purification of the Pigment Controlling Photoresponsive Development of Plants." Proc. Nat. Acad. Sci. USA, 45, 12, 1703-1708.

39. Carpenter, B., Hamner, K.C. 1963. "Effect of Light Quality on Rhythmic Flowering Response of Biloxi Soybean." Plant Physiol.,

38, 6, 698-703.

40. Cathey, H.M., Borthwick, H.A. 1957. "Photoreversibility of Floral Initiation of Chrysanthemum." Bot. Gaz., 119, 2, 71-76.

41. Cathey, H.M., Borthwick, H.A. 1964. "Significance of Dark Reversion of Phytochrome in Flowering of Chrysanthemum Morifolium." Bot. Gaz., 125, 4, 232-236.

42. DeLint, P.J.A.L., Sprüit, C.J.P. 1963. "Phytochrome Destruction Following Illumination of Mesocotyls of Zea Mays L." Meded. Landbouwhogeschool Wageningen, 63, 14, 1-7.

43. Downs, R.J. 1955. "Photoreversibility of Leaf and Hypocotyl Elongation of Darkgrown Red Kidney Bean Seedlings." Plant Physiol., 30, 5, 468-472.

44. Downs, R.J. 1956. "Photoreversibility of Flower Initiation." Plant Physiol., 31, 4, 279-284.

45. Downs, R.J. 1959. "Photocontrol of Vegetative Growth." In: Photoperiodism and Related Phenomena in Plant and Animals, Washington, p. 129-135.

46. Downs, R.J. 1961. "Photocontrol of Anthocyanin Synthesis in Darkgrown Milo Seedlings." Plant Physiol., 36, Suppl., 42.

47. Downs, R.J. 1964. "Photocontrol of Anthocyanin Synthesis." J. Wash. Acad. Sci., 54, 4, 112-120.

48. Downs, R.J. 1964. "Photocontrol of Germination of Seeds of the Bromeliaceae." Fython, 21, 1, 1-6.

49. Downs, R.J., Borthwick, H.A. 1956. "Effects of Photoperiod on Growth of Trees." Bot. Gaz., 117, 5, 310-326.

50. Downs, R.J., Cathey, H.M. 1960. "Effects of Light, Gibberellin and a Quaternary Ammonium Compound on the Growth of Darkgrown Red Kidney Beans." Bot. Gaz., 121, 4, 233-236

51. Downs, R.J., Hendricks, S.B., Borthwick, H.A. 1957. "Photoreversible Control of Elongation of Pinto Beans and Other Plants under Normal Conditions of Growth." Bot. Gaz., 118, 4, 199-208.

52. Downs, R.J., Piringer, A.A. 1958a. "Comparison of Incandescent and Fluorescent Lamps for Lengthening Photoperiods." Proc. Amer. Soc. Hortic. Sci., 71, 568-578.

53. Downs, R.J., Piringer, A.A. 1958b. "Effects of Photoperiod and Kind of Supplemental Light on Vegetative Growth of Pines." Forest Sci., 4, 3, 185-195.

54. Downs, R.J., Siegelman, H.W. 1963. "Photocontrol of Anthocyanin Synthesis in Milo Seedlings." Plant Physiol., 38, 1, 25-30.

55. Eagles, C.F., Wareing P.F. 1964. "The Role of Growth Substances in the Regulation of Bud Dormancy." Physiol. plantarum, 17, 3, 697-709.

56. Eberhardt, F. 1954. "Über die Beziehung zwischen Atmung und Anthocyansynthese." Planta, 43, 4, 253-287.

57. Evenari, M., Neumann, G., Blumenthal-Goldschmidt, C., Mayer, A.M., Poljakoff-Mayber, A. 1958. "The Influence of Gibberellic Acid and Kinetin on Germination and Seedling Growth of Lettuce." Bull. Res. Council. Israel, D, 6, 2, 65-72.

58. Evenari, M., Neumann, G., Klein, S. 1955. "The Influence of Red and Infrared Light on the Respiration of Photoblastic Seed." Physiol. plantarum, 8, 1, 33-47.

59. Fletcher, R.A., Zalik, S. 1964. Effect of Light Quality on Growth and Free Indole-Acetic Acid Content in Phaseolus Vulgaris." Plant Physiol., 39, 3, 328-331.

60. Flint, L.H., McAlister, E.D. 1937. "Wave Lengths of Radiation in the Visible Spectrum Promoting the Germination of Light Senstive Lettuce Seed." Smithsonian Inst. Publs. Misc. Collect., 96, 1-8. (Cited by Parker, Hendricks, Borthwick, Scully, 1945).

61. Fredericq, H. 1964. "Conditions Determining Effects of Far-Red Irradiations on Flowering Response of Pharbitis Nil." Plant Physiol., 39, 5, 812-816.

62. Friend, D.J.C. 1964. "The Promotion of Floral Initiation of Wh[illegible] by Far-Red Radiation." Physiol. plantarum, 17, 4, 909-920.

63. Friend, D.J.C. 1965. "Interaction of Red and Far-Red Radiations with the Vernalization Process in Winter Rye." Canad. J. Bot., 43, 1, 161-170.

64. Furuya, M., Hillman, W.S. 1964. "Observations on Spectrophotometrically Assayable Phytochrome in Vivo in Etiolated Pisum Seedlings." Planta, 63, 1, 31-42.

65. Furuya, M., Thomas, R.E. 1962. "Control of Biosynthesis of Kaempferol Complexes and of Growth by Red and Far-Red Light in Etiolated Peas." Plant Physiol., 37, Suppl., XXVIII.

66. Furuya, M., Thomas, R.G. 1964. "Flavonoid Complexes in Pisum Sativum. 11. Effects of Red and Far-Red Light on Biosynthesis of

Kaempferol Complexes and on Growth of Etiolated Plumules." Plant Physiol., 39, 4, 634-642.

67. Furuya, M., Torrey, J.G. 1964. "The Reversible Inhibition by Red and Far-Red Light of Auxin-Induced Lateral Root Initiation in Isolated Pea Roots." Plant Physiol., 39, 6, 987-991.

68. Galston, A.W. 1959. "Studies on Indoleacetic Acid Oxidase Inhibitor and Its Relation to Photomorphogenesis." In: Photoperiodism and Related Phenomena in Plant and Animals. Washington, p. 137-157.

69. Galston, A.W., Baker, R.S. 1953. "Studies on the Physiology of Light Action. V. Photoinductive Alteration of Auxin Metabolism in Etiolated Peas." Amer. J. Bot., 40, 6, 512-516.

70. Galston, A.W., Hand, M.E. 1949. "Studies on the Physiology of Light Acttion. I. Auxin and the Light Inhibition of Growth." Amer. J. Bot., 36, 1, 85-94.

71. Gordon, S.A. 1964. "Oxidative Phosphorylation as a Photomorphogenic Control." Quart. Rev. Biol., 39, 1, 11-18.

72. Gordon, S.A., Surrey, K. 1958. "Red, Far-Red Interaction in Oxidative Phosphorylation." Plant Physiol., 33, Suppl., XXIV.

73. Gordon, S.A., Surrey, K. 1960. "Red and Far-Red Action on Oxidative Phosphorylation." Radiat. Res., 12, 4, 325-339.

74. Haber, A.H., Luippold, H.J. 1960. "Effects of Gibberellin, Kinetin, Thiourea, and Photomorphogenic Radiation on Mitotic Activity in Dormant Lettuce Seed." Plant Physiol., 35, 4, 486-494.

75. Haber, A.H., Tolbert, N.E. 1959. "Effects of Gibberellic Acid, Kinetin, and Light on the Germination of Lettuce Seed." In: Photoperiodism and Related Phenomena in Plants and Animals, Washington, p. 197-206.

76. Häcker, M., Hartmann, K.M., Mohr, H. 1964. "Zellteilung und Zellwachstum im Hypokotyl von Lactuca sativa L. unter dem Einfluss des Lichtes." Planta, 63, 3, 253-268.

77. Hagen, C.E., Borthwick, H.A., Hendricks, S.B. 1954. "Oxygen Consumption of Lettuce Seed in Relation to Photocontrol of Germination." Bot. Gaz., 115, 4, 360-364.

78. Hahn, J.M. 1959. "Morphologische und wirkstoffphysiologische Untersuchungen an Pflanzen, die bei ausschliesslich künstlichem Licht herangezogen wurden. I, II." Gartenbauwissenschaft, 24, 2, 229-264, N 3, 363-410.

79. Hamner, K.C., Takimoto, A. 1964. "Circadian Rhythms and Plant Photoperiodism." Amer. Naturalist, 98, 902, 295-322.

80. Harraschain, H., Mohr, H. 1963. Der Einfluss sichtbarer Strahlung auf die Flavonoidsynthese und Morphogenese der Buchweizenkeimlinge (Fagopyrum esculentum Moench.). II. Flavonolsynthese und Hypokotylwachstum." Z. Bot., 51, 3, 277-299.

81. Hendricks, S.B. 1960. "The Photoreactions Controlling Photoperiodism and Related Responses." In: Comparative Biochemistry of Photoreactive Systems, Vol 1, p. 303-321.

82. Hendricks, S.B. 1963. "Metabolic Control of Timing. Photoperiodic and Rhythmic Responses in Plants and Animals Depend on Control of Metabolism by Light." Science, 141, 3575, 21-27.

83. Hendricks, S.B. 1964. "Photochemical Aspects of Plant Photoperiodicity." In: Photophysiology, Vol 1, N.Y.

84. Hendricks, S.B., Borthwick, H.A. 1959a. "Photocontrol of Plant Development by the Simultaneous Excitations of Two Interconvertible Pigments." Proc. Nat. Acad. Sci. USA, 45, 3, 344-349.

85. Hendricks, S.B., Borthwick, H.A. 1959b. "Photocontrol of Plant Development by the Simultaneous Excitation of Two Interconvertible Pigments. II. Theory and Control of Anthocyanin Synthesis." Bot. Gaz., 120, 4, 187-193.

86. Hendricks, S.B., Borthwick, H.A. 1963. "Control of Plant Growth by Light." In: Environmental Control of Plant Growth, N.Y., p. 233-263.

87. Hendricks, S.B., Toole, E.H., Toole, V.K., Borthwick, H.A. 1959. "Photocontrol of Plant Development by the Simultaneous Excitations of Two Interconvertible Pigments. III. Control of Seed Germination and Axis Elongations." Bot. Gaz., 121, 1, 1-8.

88. Henshall, J.D., Goodwin, T.W. 1964. "Amino Acid-Activating Enzymes in Germinating Pea Seedlings." Phytochemistry, 3, 6, 677-691.

89. Hess, D. 1959. "Die selecktive Blockierung eines an der Blühinduktion beteiligten Ribosenucleinsäure-Eiweiss-Systems durch 2-Thiouracil. (Untersuchungen an Streptocarpus wendlandii)." Planta, 54, 1, 74-94.

90. Hess, D. 1961a. "Die Beteiligung spezifischer Ribonucleinsäure an der Blühinduktion." Planta, 57, 1, 13-28.

91. Hess, D. 1961b. "Der Status der vegetativtätigen Ribonucleinsäure während der Blühinduktion." Planta, 57, 1, 29-43.

92. Hess, D. 1964. "Die Beteiligung von Ribonucleinsäure an der gengesteuerten Induktion der Anthrocyansynthese bei Petunia." Planta, 61, 1, 73-89.

93. Hillman, W.S. 1957. "Nonphotosynthetic Light Requirement in Lemna Minor and Its Partial Satisfaction by Kinetin." Science, 126, 3265, 165-166.

94. Hillman, W.S. 1959. "Interaction of Growth Substances and Photoperiodically Active Radiants on the Growth of Pea Internode Sections." In: Photoperiodism and Related Phenomena in Plants and Animals, Washington, p. 181-196.

95. Hillman, W.S. 1964. "Phytochrome Levels Detectable by in Vivo Spectrophotometry in Plant Parts Grown or Stored in the Light." Amer. J. Bot., 51, 10, 1102-1107.

96. Hillman, W.S., Galston, A.W. 1957. "Inductive Control of Indoleacetic Acid Oxidase Activity by Red and Near-Infrared Light." Plant Physiol., 32, 2, 129-135.

97. Hock, B., Mohr, H. 1964. "Die Regulation der O_2-Aufnahme von Senfkeimlingen (Sinapis alba L.) durch Licht." Planta, 61, 3, 209-228.

98. Hotta, Y. 1960. "The Role of Protein and Ribonucleic Acid in the Differentiation of Fern Gametophyte." Jap. J. Bot., 17, 2, 214-229.

99. Humphries, E.C., Wheeler, A.W. 1960. "The Effects of Kinetin, Gibberellic Acid and Light on Expansion and Cell Division in Leaf Disks of Dwarf Bean (Phaseolus Vulgaris)." J. Exp. Bot., 11, 31, 81-86.

100. Ikuma, H., Thimann, K.V. 1960. "Action of Gibberellic Acid on Lettuce Seed Germination." Plant Physiol., 35, 5, 557-566.

101. Ikuma, H., Thimann, K.V. 1963a. "Action of Kinetin on Photosensitive Germination of Lettuce Seed as Compared with that of Gibberellic Acid." Plant Cell Physiol., 4, 1, 113-128.

102. Ikuma, H., Thimann, K.V. 1963b. "The Role of the Sed-Coats in Germination of Photosensitive Lettuce Seeds." Plant Cell Physiol., 4, 2, 169-185.

103. Ikuma, H., Thimann, K.V. 1963b. "Activity of Gibberellin 'D' on the Germination of Photosensitive Lettuce Seeds." Nature, 197, 4874, 131-1314.

104. Ikuma, H., Thimann, K.V. 1964. "Analysis of Germination Processes of Lettuce Seed by Means of Temperature and Anaerobiosis." Plant Physiol., 39, 5, 756-767.

105. Jacopi, Z. 1964. "Influenza della luce sulla germinazione di semi di alune plants forestali." Ricerca scient., Pt. 2, Ser. B, 4, 4, 481-484.

106. Kahn, A., Goss, J.A., Smith, D.E. 1957. "Effect of Gibberellin on Germination of Lettuce Seed." Science, 125, 3249, 645-646.

107. Kandeler, R. 1960. "Über die Lichtabhängigkeit der Anthocyanbildung." Flora, 149, 4, 487-519.

108. Kandeler, R. 1962. "Die Aufhebung der photoperiodischen Steuerung bei Lemna gibba." Ber Deutsch. bot. Ges., 75, 10, 431-442.

109. Kandeler, R. 1963. "Phytochrom-Wirkung auf die vegetative Entwiclung von Lemna gibba." Naturwissenschaften, 50, 16, 551-552.

110. Kasperbauer, M.J., Borthwick, H.A., Hendricks, S.B. 1963. "Inhibition of Flowering of Chenopodium Rubrum by Prolonged Far-Red Radiation." Bot. Gaz., 124, 6, 444-451.

111. Kasperbauer, M.J., Borthwick, H.A. 1964. "Photoreversibility of Stem Elongation in Melitotus Alba. Desr." Crop. Sci., 4, 1, 42-44.

112. Kefford, N.P. 1962. "Auxin-Gibberellin Interaction in Rice Coleoptile Elongation." Plant Physiol., 37, N 3, 380-386.

113. Klein, A.O., Hagen, C.W. 1961. "Anthocyanin Production in Detached Petals of Impatiens Balsamina L." Plant Physiol., 36, 1, 1-9.

114. Klein, S., Preiss, J.W. 1958. "Reversibility of the Red-Far-Red Reaction by Irradiation at Different Sites." Nature, 181, 4603, 200-201.

115. Klein, W.H. 1959. "Interaction of Growth Factors with Photoprocess in Seedling Growth." In: Photoperiodism and Related Phenomena in Plant and Animals, Washington, p. 207-215.

116. Klein, W.H., Withrow, R.B., Elstad, V.B. 1956. "Response of the Hypocotyl Hook of Bean Seedlings to Radiant Energy and Other Factors." Plant Physiol., 31, 4, 289-294.

117. Klein, W.H., Withrow, R.B., Elstad, V., Price, L. 1957. "Photocontrol of Growth and Pigment Synthesis in the Bean Seedling as Related to Irradiance and Wave Length." Amer. J. Bot., 44, 1, 15-19.

118. Könitz, W. 1958. "Blühhemmung bei Kurztagpflanzen durch Hellrot- und Dunkelrotlicht in der photo- und skotophilen Phase." Planta, 51, 1, 1-29.

119. Landgraf, J.E. 1961. "Über den Einfluss des Lichts auf den

Proteinstoffwechsel bei Keimlingen von Sinapis alba L." Planta, 57, 5, 543-556.

120. Lane, H.C. 1963. "Effect of Light Quality on Maturity in the Milo Group of Sorghum." Crop Sci., 3, 6, 496-499.

121. Lane, H.C., Kasperbauer, M.J. 1965. "Photomonphogenic Responses of Dodder Seedlings." Plant Physiol., 40, 1, 109-116.

122. Land, H.C., Siegelman, H.W., Butler, W.L., Firer, E.M. 1963. "Detection of Phytochrome in Green Plants." Plant Physiol., 38, 4, 414-416.

123. Leopold, A.C., Guernsey, F.S. 1954. "Respiratory Responses to Red and Infra-Red Light." Physiol. plantarum, 7, 1, 30-40.

124. Liverman, J.L. 1959. "Control of Leaf Growth by an Interaction of Chemicals and Light." In: Photoperiodism and Related Phenomena in Plants and Animals, Washington, p. 161-180.

125. Liverman, J.L., Bonner, J. 1953. "The Interaction of Auxin and Light in the Growth Responses of Plants." Proc. Nat. Acad. Sci. USA, 39, 9, 905-916.

126. Liverman, J.L., Johnson, S.P. 1958. "The Control of Plant Growth by an Interaction of Light and Chemicals." Scientia, 93, 11, 293-295.

127. Lockhart, J.A. 1956. "Reversal of the Light Inhibition of Pea Stem Growth by the Gibberellins." Proc. Nat. Acad. Sci. USA, 42, 11, 841-848.

128. Lockhart, J.A. 1958a. "The Response of Various Species of Higher Plants to Light and Gibberellic Acid." Physiol. plantarum, 11, 3, 478-486.

129. Lockhart, J.A. 1958b. "The Influence of Red and Far-Red Radiation on the Response of Phaseolus Vulgaris to Gibberellic Acid." Physiol. plantarum, 11, 3, 487-492.

130. Lockhart, J.A. 1959a. "Studies on the Mechanism of Stem Growth Inhibition by Visible Radiation." Plant Physiol., 34, 4, 457-460.

131. Lockhart, J.A. 1959b. "Control of Stem Growth by Light and Gibberellic Acid." In: Photoperiodism and Related Phenomena in Plant and Animals, Washington, p. 217-221.

132. Lockhart, J.A. 1961. "Interaction between Gibberellin and Various Environmental Factors on Stem Growth." Amer. J. Bot., 48, 6, 516-525.

133. Lockhart, J.A., Gottschall, V. 1959. "Growth Responses of Alaska Pea Seedlings to Visible Radiation and Gibberellic Acid." Plant Physiol., 34, 4, 460-465.

134. Lörcher, L. 1958. "Die Wirkung verschiedener Lichtqualitäten auf der endogene Tagesrhythmik von Phaseolus." Z. Bot., 46, 2-3, 209-241.

135. Marcus, A. 1960. "Photocontrol of Formation of Red Kidney Bean Leaf Triphosphopyridine Nucleotide Linked Triosephosphate Dehydrogenase." Plant Physiol., 35, 1, 126-128.

136. Marcus, A., Feeley, J. 1964. "Activation of Protein Synthesis in the Inhibition Phase of Seed Germination." Proc. Nat. Acad. Sci. USA, 51, 6, 1075-1079.

137. Margulies, M.M. "Effect of Chloramphenicol on Light Dependent Development of Seedlings of Phaseolus Vulgaris var. Black Valentine, with Particular Reference to Development of Photosynthetic Activity." Plant Physiol., 37, 4, 473-480.

138. Margulies, M.M. 1964. "Effects of Chloramphenicol on Light-Dependent Synthesis of Proteins and Enzymes of Leaves and Chloroplasts of Phaseolus Vulgaris." Plant Physiol., 39, 4, 579-585.

139. Margulies, M.M. 1965. "Relationship between Red Light Mediated Glyceraldehyde-3-phosphate Dehydrogenase Formation and Light Dependent Development of Photosynthesis." Plant Physiol., 40, 1, 57-61.

140. Metche, M., Gay, R. 1964. "Zur Biogenese der anthocyanischen Pigmente." Brauwissenschaft, 17, 9, 347-351.

141. Miller, C.O. 1956. "Similarity of Some Kinetin and Red Light Effects." Plant Physiol., 31, 4, 318-319.

142. Miller, C.O. 1958. "The Relationship of the Kinetin and Red-Light Promotions of Lettuce Seed Germination." Plant Physiol., 33, 2, 115-117.

143. Mitrakos, K. "The Participation of the Red-Far-Red Reaction System in Chlorophyll Metabolism." Physiol. plantarum, 14, 3, 497-503.

144. Moh, C.C., Withrow, R.B. 1959. "Nonionizing Radiant Energy as an Agent in Altering the Incidence X-ray-Induced Chromatid Aberrations. II. Reversal of the Far-Red Potentiating Effect in Vicia by Red Radiant Energy." Radiat. Res., 10, 1, 13-19.

145. Mohr, H. 1957. "Der Einfluss monochromatischer Strahlung auf das Längenwachstum des Hypokotyls und auf die Anthocyanbildung bei Keimlingen von Sinapis alba L. (Brassica alba Boiss.)." Planta,

49, 4, 389-435.

146. Mohr, H. 158. "Neue Studien über morphogenetisch wichtige Pigmentsysteme in Pflanzen." Naturwissenschaften, 45, 18, 448-449.

147. Mohr, H. 1959a. "Der Lichteinfluss auf die Haarbildung am Hypokotyl von Sinapis alba L." Planta, 53, 2, 109-124.

148. Mohr, H. 1959b. "Der Lichteinfluss auf das Wachstum der Keimblätter bei Sinapis alba L." Planta, 53, 3, 219-245.

149. Mohr, H. 1960. "Photomorphogenetische Reaktionssysteme in Pflanzen. I. Das reversible Hellrot-Dunkelrot-Reaktionssystem und das Blau-Dunkelrot-Reaktionssytem." Ergebn. Biol., 22, 67-107.

150. Mohr, H. 1962. "Primary Effect of Light on Growth." Ann. Rev. Plant Physiol., 13, 465-488.

151. Mohr, H. 1964. "The Control of Plant Growth and Development by Light." Biol. Rev. Cambridge Philos. Soc., 39, 1, 87-112.

152. Mohr, H. 1965. "Steuerung der pflanzlichen Entwicklung durch Licht." Naturwiss. Rundschau, 18, 3, 101-108.

153. Mohr, H., Appuhn, U. 1962. "Die Steuerung des Hypocotylwachstums von Sinapis alba L. durch Licht und Gibberellinsäure." Planta, 59, 1, 49-67.

154. Mohr, H., Appuhn, U. 1963. "Die Keimung von Lactuca-Achänen unter dem Einfluss des Phytochromsystems und der Hochenergiereaktion der Photomorphogenese." Planta, 60, 3, 274-288.

155. Mohr, H., Haug, A. 1962. "Die histologischen Vorgänge während der lichtabhängigen Schliessung und Öffnung des Plumulahakens bei den Keimlingen von Lactuca sativa L." Planta, 59, 2, 151-164.

156. Mohr, H., Nes, E. van. 1963. "Der Einfluss sichtbarer Strahlung auf die Flavornoidsynthese und Morphogenese der Buchweizen-Keimlinge (Fagopyrum esculentum Moench.). I. Synthese von Anthocyan." Z. Bot., 51, 1, 1-16.

157. Mohr, H., Noble, A. 1960. "Die Steuerung der Schliessung und Öffnung des Plumula-Hakens bei Keimlingen von Lactuca sativa durch sichbare Strahlung." Planta, 55, 3, 327-342.

158. Mohr, H., Pichler, J. 1960. "Der Einfluss hellroter und dunkelroter Strahlung auf die geotropische Reaktion der Keimlinge von Sinapis alba L." Planta, 55, 1, 57-66.

159. Mohr, H., Pinnig, E. 1962. "Der Einfluss des Lichtes auf die Bildung von Blattprimordien am Vegatationskegel der Keimlinge von Sinapis alba L." Planta, 58, 6, 569-579.

160. Mumford, F.E., Smith, D.H., Castle, J.E. 1961. "An Inhibitor of Indoleacetic Acid Oxidase from Pea Tips." Plant Physiol., 36, 6, 752-756.

161. Nakayama, S., Borthwick, H.A., Hendricks, S.B. 1960. "Failure of Photoreversible Control of Flowering in Pharbitis Nil." Bot. Gaz., 121, N 4, 237-243.

162. Neyland, M., Ng, Y.L., Thimann, K.V. 1963. "Formation of Anthocyanin in Leaves of Kalanchoe Blossfeldiana -- a Photoperiodic Response." Plant Physiol., 38, 4, 447-451.

163. Nooden, L.D., Thimann, K.V. 1965. "Inhibition of Protein Synthesis and of Auxin-Induced Growth by Chloramphenicol." Plant Physiol., 40, 1, 193-201.

164. Nwachuku, N.J.C., Lockhart, J.A. 1964. "Hypocotyl Elongation in Mustard and Mung Bean Seedlings as Influenced by Light, Gibberelline, and Chlorocholine Chloride." Physiol. plantarum, 17, 3, 725-736.

165. Nyman, B. 1963. "Studies on the Germination in Seeds of Scots Pine (Pinus Silvestris L.) with Special Reference to the Light Factor." Studia forest suec., 2, 1-164.

166. Oota, Y. 1964. "RNA in Developing Plant Cells." Arn. Rev. Plant Physiol., 15, 17-36.

167. Osborne, D.J. 1965. "Interactions of Hormonal Substances in the Growth and Development of Plants." J. Sci. Food and Agric., 16, 1, 1-13.

168. Parker, M.W., Hendricks, S.B., Borthwick, H.A. 1950. "Action Spectrum for the Photoperiodic Control of Floral Initiation of the Long-Day Plant, Hyoscyamus Niger." Bot Gaz., 111, 3, 242-252.

169. Parker, M.W., Hendricks, S.B., Borthwick, H.A., Scully, N.J. 1945. "Action Spectrum for Photoperiodic Control of Flower Initiation in Biloxi Soybean." Science, 102, 152-155.

170. Parker, M.W., Hendricks, S.B., Borthwick, H.A., Scully, N.J. 1946. "Action Spectra for Photoperiodic Control of Floral Initiation in Short-Day Plants." Botan. Gaz., 108, 1, 1-26.

171. Parker, M.W., Hendricks, S.B., Borthwick, H.A., Went, F.W. 1949. "Spectral Sensitivities for Leaf and Stem Growth of Etiolated Pea Seedlings and Their Similarity to Action Spectra for Photoperiodism."

Amer. J. Bot., 36, 2, 194-204.

172. Phillips, I.D.J., Vlitos, A.J., Cutler, H. 1959. "The Influence of Gibberellic Acid upon the Endogenous Growth Substances of the Alaska Pea." Contrib. Boyce Thomps. Inst., 20, 2, 111-120.

173. Piringer, A., Heinze, P. 1954. "Effect of Light on the Formation of a Pigment in the Tomato Fruit Cuticle." Plant Physiol., 29, 5, 467-472.

174. Powell, R.D., Griffith, M.M. 1960. "Some Anatomical Effects of Kinetin and Red Light on Disks of Bean Leaves." Plant Physiol., 35, 2, 273-275.

175. Price, L., Klein, W.H. 1961. "Red, Far-Red Response and Chlorophyll Synthesis." Plant Physiol., 36, 6, 733-735.

176. Price, L., Mitrakos, K., Klein, W.H. 1964. "Photomorphogenesis and Carbohydrate Changes in Etiolated Leaf Tissue." Quart. Rev. Biol., 39, 1, 11-18.

177. Robinson, P.M., Wareing, P.F, 1964. "Chemical Nature and Biological Properties of the Inhibitor Varying with Photoperiod in Sycamore (Acer Pseudoplatanus)." Physiol. plantarum, 17, 2, 314-323.

178. Roesel, H.A., Haber, A.H. 1963. "Studies of Effects on Growth Pattern and of Gibberellin Sensitivity in Relation to Age, Growth rate and Illumination in Intact Wheat Coleoptiles." Plant Physiol., 38, 5, 523-532.

179. Rollin, P. 1963. "Observations sur la difference de nature de deux photoreactions controlant la germination des akenes de Lactuca sative var. 'Reine de Mai.' C.R. Acad. Sci. Paris, 257, 23, 3642-3645.

180. Rollin, P. 1964a. "Influence de la lumiere sur la morphogenese des vegetaux." Annee biol., 3, 3-4, 95-135.

181. Rollin, P. 1964b. "Les reactions de photomorphogenese chez les plantules de Phacelia tanacetifolia." Ann. physiol. veget., 6, 1, 5-16.

182. Rollin, P. 1964c. "Remarques concernant l'action de la lumiere sur la germination." Canad. J. Bot., 42, 4, 463-471.

183. Ruge, U. 1960. "Der Auxin-Gehalt von Tradescantia-Blättern in Abhängigkeit bereichen." Naturwissenschaften, 40, 7, 225-226.

184. Ruge, U. 1960. "Der Auxin-Gehalt von Tradescantia-Blättern in Abhängigkeit von der Wellenlänge des Lichtes." Natur-

wissenschaften, 47, 16, 381-382.

185. Sale, P.J.M., Vince, D. 1960. "Effects of Light and Gibberellic Acid on Internode Growth in Pisum Sativum." Physiol. plantarum, 13, 4, 664-673.

186. Salisbury, F.B., Bonner, J. 1960. "Inhibition of Photoperiodic Induction by 5-Fluorouracil." Plant Physiol., 35, 2, 173-177.

187. Scharff, O. 1962. "Effects of Red and Far-Red Light on the Hypocotyl of Picea Abies." Physiol. plantarum, 15, 4, 804-814.

188. Schrank, A.R. 1957. "Stimulation of Avena Coleoptile Growth by Kinetin and Some of Its Analogs." Plant Physiol., 32, Suppl., XLIX.

189. Scott, R.A., Liverman, J.L. 1956. "Promotion of Leaf Expansion by Kinetin and Benzylaminopurine." Plant Physiol., 37, 4, 321-322.

190. Scott, R.A., Jr., Liverman, J.L. 1957. "Control of Etiolated Bean Leaf-Disk Expansion by Gibberellins and Adenine." Science, 1957, 126, 3264, 122-123.

191. Selman, J.W., Ahmed, E.O.S. 1962. "Some Effects of Far-Red Irradiation and Gibberellic Acid on the Growth of Tomato Plants." Ann. Appl. Biol., 50, 479-485.

192. Siegelman, H.W., Firer, E.M. 1964. "Purification of Phytochrome from Oat Seedlings." Biochemistry, 3, 3, 418-423.

193. Siegelman, H.W., Hendricks, S.B. 1957. "Photocontrol of Anthocyanin Formation in Turnip and Red Cabbage Seedlings." Plant Physiol., 32, 5, 393-398.

194. Siegelman, H.Q., Hendricks, S.B. 1958a. "Photocontrol of Anthocyanin Synthesis in Apple Skin." Plant Physiol., 33, 3, 185-190.

195. Siegelman, H.W., Hendricks, S.B. 1958b. "Photocontrol of Alcohol, Aldehyde and Anthocyanin Production in Apple Skin." Plant Physiol., 33, 6, 409-413.

196. Simpson, G.M., Wain, R.L. 1961. "A Relationship Between Gibberellic Acid and Light in the Control of Internode Extension of Swarf Peas (Peasum Sativum). J. Exp. Bot., 12, 35, 207-216.

197. Sisler, E.C., Klein, W.H. 1961. "Effect of Red and Far-Red Irradiation on Nucleotide Phosphate and Adenosine Triphosphate Levels in Dark-Grown Bean and Avena Seedlings." Physiol. plantarum, 14, 1, 115-123.

198. Stafford, H.A. 1965. "Flavonoids and Related Phenolic Compounds Produced in the First Internode of Sorghum Vulgare Pers. in Darkness and in Light." Plant Physiol., 40, 130-138.

199. Surgiura, M. 1963. "Effect of Red and Far-Red Light on Protein and Phosphate Metabolism in Tobacco Leaf Disks." Bot. Mag., Tokyo, 76, 899, 174-180.

200. Surrey, K. 1962. "Action and Interaction of Monochromatic Light on Phosphate Metabolism in Germination of Lettuce Seeds." Canad. J. Bot., 40, 7, 965-974.

201. Surrey, K., Gordon, S.A. 1962. "Influence of Light on Phosphate Metabolism in Lettuce Seed: Spectral Response Red, Far-Red Interaction." Plant Physiol., 37, 3, 327-332.

202. Takimoto, A., Hamner, K.C. 1964. "Effect of Temperature and Preconditioning on Photoperiodic Response of Pharbitis Nil." Plant Physiol., 39, 6, 1024-1030.

203. Takimoto, A., Ikeda, K. 1959. "Studies in the Light Controlling Photoperiodic Induction of Pharbitis Nil. II. Effect of Far-Red Light Preceding the Inductive Dark Period." Bot. Mag., Tokyo, 72, 851, 181-189.

204. Takimoto, A., Naito, Y. 1962. "Studies on the Light Controlling Flower Initiation of Pharbitis Nil. IX. Further Studies on the Effect of Far-Red Light Preceding the Inductive Dark Period." Bot. Mag., Tokyo, 75, 888, 205-211.

205. Thimann, K.V., Radner, B.S. 1955. "The Biogenesis of Anthocyanins. IV. The Inhibitory Effect of Methionine and Other Sulfur-Containing Compounds on Anthocyanin Formation." Arch. Biochem. and Biophys., 58, 2, 484-497.

206. Thimann, K., Radner, B. 1955. "The Biogenesis of Anthocyanins. V. Evidence for the Mediation of Pyrimidines in Anthocyanin Synthesis." Arch. Biochem. and Biophys., 59, 2, 511-525.

207. Thomson, B.F. 1954. "The Effect of Light on Cell Division and Cell Elongation in Seedlings of Oats and Peas." Amer. J. Bot., 41, 4, 326-332.

208. Thomson, B.F. 1959. "Far-Red Reversal of Internode-Stimulating Effect of Red Light on Peas." Amer. J. Bot., 46, 10, 740-742.

209. Thomson, B.F., Miller, P.M. 1961. "Growth Patterns of Pea Seedlings in Darkness and in Red and White Light." Amer. J. Bot., 48, 3, 256-261.

210. Thomson, B.F., Miller, P.M. 1963. "The Role of Light in Histogenesis and Differentiation in the Shoot of Pisum Sativum. III. The Internode." Amer. J. Bot., 50, 3, 219-227.

211. Toole, E.H., Show, A.G. Jr., Tools, V.K., Borthwick, H.A. 1956. "Effects of Light and Temperature on Germination of Virginia Pine Seeds." Plant Physiol., 31, Suppl., XXXVI.

212. Toole, E.H., Toole, V.K., Borthwick, H.A., Hendricks, S.B. 1955. "Photocontrol of Lepidium Seed Germination." Plant Physiol., 30, 1, 15-21.

213. Varner, J.E. 1964. "Gibberellic Acid Controlled Synthesis of Alfa-Amylase in Barley Endosperm" Plant Physiol., 39, 3, 413-415.

214. Varner, J.E., Chandra, G.R. 1964. "Hormonal Control of Enzyme Synthesis in Barley Endosperm." Proc. Nat. Acad. Sci. USA, 52, 1, 100-106.

215. Virgin, H.J. 1957. "Chlorophyll a Content and Transpiration of Etiolated Wheat Leaves after Pretreatment with a Short Light Impulse Followed by Dark Periods of Varying Lengths." Physiol. plantarum, 10, 2, 445-453.

216. Virgin, H.J. 1958. "Studies on the Formation of Protochlorophyll and Chlorophyll a under Varying Light Treatments." Physiol. plantarum, 11, 2, 347-362.

217. Vlitos, A.J., Meudt, W. 1957. "The Effect of Light and of the Shoot Apex on the Action of Gibberellic Acid." Contribs. Boyce Thomps. Inst., 79, 1, 55-62.

218. Wagne, C. 1964. "The Distribution of the Light-Effect in Partly Irradiated Grass Leaves." Physiol. plantarum, 17, 3, 751-756.

219. Webster, G.C. 1961. "Protein Synthesis." Ann. Rev. Plant Physiol., 12, 113-132.

220. Weisz, J. 1960. "Action des temperatures relativement basses sur la germination dans la kinetine des semences de Laitue, variete 'Grand Rapids.'" C.R. Acad. Sci., Paris, 251, 1, 125-127.

221. Went, F.W. 1941. "Effects of Light on Stem and Leaf Growth." Amer. J. Bot., 28, 2, 83-95.

222. Wilkins, M.B., Goldsmith, M.H.M. 1964. "The Effects of Red, Far-Red, and Blue Light on the Geotropic Response of Coleoptiles of Zea Mays." J. Exp. Bot., 15, 45, 600-615.

223. Withrow, R.B., Klein, W.H., Elstad, V.B. 1957. "Action

Spectra of Photomorphogenic Induction and Its Photoinactivation." Plant Physiol., 32, 4, 453-462.

224. Withrow, R.B., Klein, W.H., Price, L., Elstad, V. 1953. "Influence of Visible and Near Infrared Radiant Energy on Organ Development and Pigment Synthesis in Bean and Corn." Plant Physiol., 28, 1, 1-14.

225. Withrow, R.B., Moh, C.C. 1957. "Nonionizing Radiant Energy as an Agent in Altering the Incidence of X-ray Induced Chromatic Aberrations. I. Effects of Far-Red and Infrared Radiant Energy on Tradescantta and Vicia." Radiat. Red., 6, 4, 491-500.

226. Zeevaart, J.A.D. 1962. "DNA Multiplication as a Requirement for Expression of Floral Stimulus in Pharbitis Nil." Plant Physiol., 37, 4, 296-304.